SEED DISPERSAL BY CHELONIANS: FROM INDIVIDUALS TO COMMUNITIES

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TO MY PARENTS (ALL FOUR OF THEM!),

FOR ENDURING MY INTEREST IN NATURE,
AND ENCOURAGING ME TO DO WHAT I LOVE,

AND TO HÉCTOR QUINTERO VÁZQUEZ,

MY HIGH SCHOOL BIOLOGY TEACHER,
WHO CULTIVATED MY INTEREST IN SCIENCE

"In the long history of humankind (and animal kind, too) those who learned to collaborate and improvise most effectively have prevailed."
–Charles R. Darwin

CONTENTS

SUMMARY

Plants are sessile for the most of their life cycle, but their gametes (pollen) and their propagules (seeds) can move from short to quite long distances across the landscape. The mechanism for the latter is called seed dispersal. Seed dispersal is the link between the end of reproduction and the beginning of vegetative growth, and is an important function that determines plant population persistence by influencing reproduction, population- and community dynamics. Many plant species rely on animal-mediated seed dispersal (zoochory), which thus ultimately shapes much of the world's biodiversity. Chelonians represent one of the oldest vertebrate lineages, and have been considered one of the early frugivores and seed dispersers in evolutionary time. However, the role of chelonians as seed dispersers has been largely neglected and underestimated until very recently, despite repeated calls for the study of chelonian frugivory and seed dispersal (FSD).

In my thesis, I assessed the role of chelonians as seed dispersers, from species to communities. I began by performing a review and synthesis of chelonian FSD in **Chapter 1**, where I mainly focused on: i) the taxonomical and geographic distribution of chelonian FSD, ii) the taxonomical distribution and traits of plants dispersed by chelonians, and iii) chelonian seed dispersal efficiency. My work is the first to provide an overview of the role of chelonians as frugivores and seed dispersers, and it highlights their importance not only from the individual and population perspective, but also from the community perspective.

In **Chapter 2** I then focused on Aldabra giant tortoises (*Aldabrachelys gigantea*) to assess their role in the seed dispersal community of Aldabra Atoll in relation to other frugivores. I provide the third study to date that evaluates the role of chelonians as seed dispersers at the community level using network analyses, and also provide the first evaluation of the role of tortoises and other dispersers in the plant–frugivore community of Aldabra Atoll. To my knowledge, my study on the Aldabra seed dispersal network is the first of its kind performed in the Western Indian Ocean – a globally important biodiversity hotspot. Furthermore, because the plant–frugivore community of Aldabra is intact and representative of the pre-anthropogenic assemblages that other islands used to have, the Aldabra network

can serve as a template for the conservation and restoration of plant–animal interactions in these islands.

In **Chapter 3**, I experimentally examined whether tortoise size and/or seed size affect their gut retention times. Gut retention time is one of the main traits that structure the spatial extent to which seeds can be dispersed. My study is one of the few that simultaneously evaluates both the effect of tortoise size and seed size on seed gut retention time. I demonstrate that both small and large tortoises can retain seeds for long periods, and thus spread seeds far and wide, further supporting studies that have highlighted the capacity of giant tortoises for restoration.

Finally, in **Chapter 4** I studied the thermoregulatory ecology of Aldabra giant tortoises, including looking at how environmental temperature may affect their role as seed dispersers, and then applied the findings about their thermoregulatory ecology in the wild to the management and husbandry of captive tortoises in **Chapter 5**. My work is the first to assess the thermoregulatory environment and ecology of Aldabra giant tortoises across temperature gradients. I successfully applied the knowledge gained through the latter work to inform the evaluation and management of the thermoregulatory environment of tortoises in Zürich Zoo, and provide methodological procedures that can be applied to other captive ectothermic species to provide an adequate thermal environment.

ZUSAMMENFASSUNG

Pflanzen sind während des größten Teils ihres Lebenszyklus sessil, aber ihre Gameten (Pollen) und ihre Fortpflanzung (Samen) verbreiten sich oft von nah bis fern über die Landschaft. Der Mechanismus für Letzteres wird Samenausbreitung genannt. Die Samenausbreitung ist das Bindeglied zwischen dem Ende der Vermehrung und dem Beginn des vegetativen Wachstums und ist eine wichtige Funktion, die den Erhalt der Pflanzenpopulation durch Beeinflussung der Reproduktions-, Bevölkerungs- und Gemeinschaftsdynamik bestimmt.

Viele Pflanzenarten setzen auf tiervermittelte Samenausbreitung (Zoochory), die letztlich einen großen Teil der Biodiversität der Welt ausmacht. Die Ordnung der Schildkröten (Chelonia) stellt eine der ältesten Wirbeltierlinien dar und wurde in der Evolution als eine der ersten Frugivoren (Früchtefresser) und Samenverteilern angesehen. Die Rolle der Schildkröten als Samenverteiler wurde jedoch bis vor kurzem weitgehend vernachlässigt und unterschätzt. Folglich gab es Forderungen nach Untersuchungen der Frugivorie und Samenausbreitung (FSA).

In meiner Dissertation habe ich die Rolle der Schildkröten als Samenverteiler von der Art bis zur Gemeinschaften untersucht. Ich begann mit einem Überblick und einer Synthese von FSA durch Schildkröten in **Kapitel 1**, mit einem Fokus auf: i) die taxonomische und geographische Verbreitung von FSA durch Schildkröten, ii) die taxonomische Verteilung und Merkmale von Pflanzen, die von Schildkröten verbreitet werden, und iii) die Effizienz der Samenausbreitung durch Schildkröten. Meine Arbeit ist die erste, die die Rolle der Schildkröten als Fruchtfresser und Samenverbreiter untersucht, zusammenfasst und ihre Bedeutung nicht nur aus der Perspektive des Individuums oder der Population, sondern auch aus der Perspektive der Lebensgemeinschaft hervorhebt.

In **Kapitel 2** habe ich mich dann auf Aldabra-Riesenschildkröten (*Aldabrachelys gigantea*) konzentriert, um ihre Rolle in der Samenverbreitungsgemeinschaft des Aldabra-Atolls in Bezug auf andere Fruchtfresser zu beurteilen. Es ist die bisher dritte Studie, welche die Rolle der Schildkröten als Samenverteiler auf kommunaler Ebene mithilfe von Netzwerkanalysen bewertet und ist auch die erste Einschätzung der Rolle von Schildkröten und anderen Samenverteilern in der Pflanzenfrugivor-Gemeinschaft des

Aldabra Atolls – ein weltweit wichtiger Hotspot für Biodiversität. Soweit ich weiß, ist meine Studie über das Netzwerk zur Verbreitung von Aldabra-Samen die erste ihrer Art im westlichen Indischen Ozean. Da die Pflanzen-Frugivor-Gemeinschaft von Aldabra außerdem repräsentativ für die vor-anthropogenen Gemeinschaften ist, die andere Inseln früher hatten, kann das Aldabra-Netzwerk als Vorlage für die Erhaltung von Pflanzen-Tier-Interaktionen auf solche Inseln dienen.

In **Kapitel 3** habe ich experimentell untersucht, ob die Größe der Schildkröten und / oder die Samengröße die Darmretentionszeit in Aldabra-Riesenschildkröten beeinflussen. Die Darmretentionszeit ist eine der Haupteigenschaften, die das räumliche Ausmaß, in dem Samen verteilt werden können, strukturiert. Dies ist eine der wenigen Studien, die gleichzeitig sowohl die Wirkung der Schildkrötengröße als auch der Samengröße auf die Darmretentionszeit bewertet. Ich zeige, dass sowohl kleine als auch große Landschildkröten Samen für lange Zeiträume behalten können und somit Samen weit und breit verbreiten. Dieses Resultat unterstützt andere Studien, die die Kapazität von Riesenschildkröten in Bezug auf die Wiederherstellung von Ökosystemen hervorgehoben haben.

Schließlich habe ich in **Kapitel 4** die thermoregulatorische Ökologie von Aldabra - Riesenschildkröten untersucht, einschließlich der Frage, wie sich die Umgebungstemperatur auf ihre Rolle als Samenverteiler auswirken könnte, und anschließend in **Kapitel 5** die Erkenntnisse über ihre thermoregulatorische Ökologie in der Wildnis auf die Haltung von Schildkröten in Gefangenschaft angewendet. Meine Arbeit ist die erste, die die thermoregulatorische Umgebung und Ökologie von Aldabra-Riesenschildkröten über Temperaturgradienten hinweg untersucht. Das Wissen, das ich durch die letztgenannte Arbeit erworben habe, konnte ich erfolgreich in die Bewertung und das Management der thermoregulatorischen Umgebung von Schildkröten im Zoo Zürich einfließen lassen und methodische Verfahren anbieten, die auf andere in Gefangenschaft lebende ektothermische Arten angewendet werden können.

RESUMEN

Las plantas son sésiles durante la mayor parte de su ciclo de vida, pero sus gametos (polen) y sus propágulos (semillas) pueden moverse a distancias cortas –y considerablemente largas también– a través del paisaje. El mecanismo para lo último se conoce como dispersión de semillas. La dispersión de semillas es el enlace entre la culminación de la reproducción y el comienzo del crecimiento vegetativo, y es una función importante que determina la persistencia de las poblaciones de plantas influenciando su reproducción y la dinámica de poblaciones y comunidades. Muchas especies de plantas dependen de la dispersión de sus semillas mediada por animales (zoocoría), y este proceso moldea gran parte de la biodiversidad del mundo. Los quelónidos (tortugas) representan uno de los linajes de vertebrados más antiguos, y han sido considerados como uno de los frugívoros y dispersores de semillas iniciales en el tiempo evolutivo. No obstante, y hasta muy reciente, el rol de los quelónidos como dispersores de semillas había sido altamente ignorado y subestimado, a pesar de repetidos llamados para estudiar la frugivoría y dispersión de semillas (FDS) por quelónidos.

En mi tesis, evalué el rol de los quelónidos como dispersores de semillas, desde el nivel de especies hasta el nivel de comunidades. Comencé haciendo una revisión y síntesis de la literatura sobre FDS por quelónidos en el **Capítulo 1**, y me enfoqué principalmente en: i) la distribución geográfica y taxonómica de la FDS por quelónidos, ii) la distribución taxonómica y características de las plantas dispersadas por quelónidos, y iii) en la eficiencia de los quelónidos como dispersores de semillas. Mi trabajo es el primero en proveer una visión general del rol de los quelónidos como dispersores de semillas, y destaca la importancia de éstos, no sólo desde la perspectiva individual y poblacional, sino también desde la perspectiva de comunidades.

En el **Capítulo 2** me enfoqué en las tortugas gigantes de Aldabra (*Aldabrachelys gigantea*) y evalué su rol en la comunidad de dispersión de semillas del atolón de Aldabra en relación con otros frugívoros. Con mi trabajo, proveo el tercer estudio hasta la fecha que evalúa el rol de los quelónidos como dispersores de semillas al nivel de comunidades usando análisis de redes, así como también la primera evaluación del rol de las tortugas gigantes y otros dispersores de semillas en

la comunidad de plantas–frugívoros en el atolón de Aldabra. Según mi conocimiento, mi estudio sobre la red de dispersión de semillas de Aldabra es el primero de su tipo realizado en el oeste del Océano Índico –un foco de biodiversidad mundialmente importante. Además, debido a que la comunidad de plantas–frugívoros de Aldabra está intacta, y es representativa del ensamblaje pre-antropogénico que otras islas solían poseer, la red de dispersión de semillas de Aldabra puede servir como un modelo para la conservación y restauración de interacciones entre plantas–animales en islas.

En el **Capítulo 3**, examiné experimentalmente si el tamaño de las tortugas y/o el tamaño de las semillas afecta el tiempo de retención de semillas en el tracto digestivo de las tortugas. El tiempo de retención de semillas es uno de los rasgos principales que estructura el grado espacial al que las semillas pueden ser dispersadas. Mi estudio es uno de los pocos que evalúa simultáneamente los efectos del tamaño de las tortugas y de las semillas en el tiempo de retención de semillas. Con mi estudio, demostré que tortugas tanto pequeñas como de gran tamaño pueden retener semillas por periodos largos, y por consiguiente, pueden dispersar semillas a grandes distancias en el paisaje, brindándole así más apoyo a los estudios que han destacado la capacidad que tienen las tortugas gigantes para la restauración.

Finalmente, en el **Capítulo 4** estudié la ecología de termorregulación de las tortugas gigantes de Aldabra, incluyendo la evaluación de cómo la temperatura ambiental puede afectar su rol como dispersores de semillas, y luego apliqué los resultados sobre su ecología de termorregulación en el estado silvestre al manejo y cuidado de tortugas en cautiverio en el **Capítulo 5**. Mi trabajo es el primero en evaluar el ambiente y la ecología termoregulatoria de las tortugas gigantes de Aldabra en diferentes gradientes de temperatura ambiental. También, apliqué con éxito el conocimiento adquirido sobre la ecología termoregulatoria de las tortugas para informar la evaluación y el manejo del ambiente termoregulatorio de las tortugas en el Zoológico de Zürich. Conjuntamente, proveo procesos metodológicos que pueden ser aplicados en otras especies de ectotermos en cautiverio para suministrarles un ambiente termal adecuado.

GENERAL INTRODUCTION

GENERAL INTRODUCTION

The diversification of plants and animals that followed the evolution of flowers, fruits and seeds, and the subsequent co-evolution of mutualistic interactions between plants and animals, is perhaps one of the most influential series of events that helped shape our ideas in ecology. For example, these evolutionary-ecological dynamics were formative for Darwin's ideas on natural selection as a driver of co-evolution between plants and animals, and as a mechanism to explain evolutionary change (Bronstein et al. 2006). These co-evolutionary patterns also inspired others to explore the ecological and evolutionary processes driven by zoochory, setting the stage for the development of modern-day seed dispersal studies (e.g., Bascompte & Jordano 2014; Connel 1971; Janzen 1970; Thoreau 1993; 2001).

Plants are sessile for the most of their life cycle, but they do move across the landscape (Shea 2007). For this, plants employ two main strategies: pollen- and seed dispersal (Fig. 1). Seed dispersal is the link between the end of the reproduction and the establishment of new vegetative growth units (Schupp 1993; Schupp et al. 2010; Wang & Smith 2002). In many areas in the tropics up to 80–90% of plants depend on animals ingesting their seeds for dispersal (endozoochory, from here on 'zoochory'; Howe & Smallwood 1982). Zoochory is thus an important ecosystem function that determines plant population persistence by influencing their reproduction, population- and community dynamics, and neutral and adaptive evolution (Howe & Smallwood 1982; Rezende et al. 2007; Robledo-Arnuncio et al. 2014; Stoner & Henry 2008). Ultimately, zoochory therefore helps shape much of the world's biodiversity (Bascompte & Jordano 2007; Howe & Smallwood 1982).

Zoochory is a process that occurs across a spatio-temporal continuum. Exactly when and where seeds are dispersed to mainly depends on the activity and movement ecology of the frugivore, and on its seed gut retention time. Thus, to understand zoochory, it is important to consider the external and internal factors that influence frugivore activity, movement and gut retention time, and the interplay between these factors. External factors include the abiotic and biotic conditions that a frugivore is exposed to in its environment; for example, the photoperiod and solar

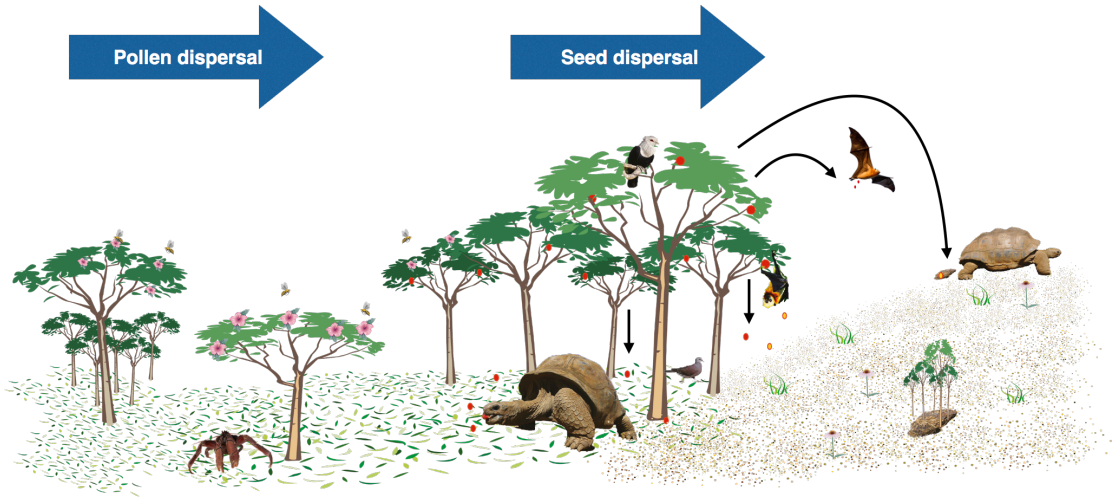

Figure 1: Pollen- and seed dispersal dynamics mediated by animals. Different animals provide different dispersal services to plants where, in the case of seeds, some may disperse them close to the mother plant, and others can disperse the seeds at medium and/or long distances (indicated by arrows). Effective seed dispersal leads to plant recruitment, and connects the end of reproduction with the recruitment of new individuals. Figure inspired by Shea (2007).

radiation, environmental temperature, humidity, distribution of food resources, and intra- and interspecific competition. Internal factors reflect the internal state of the frugivore; for example, physiological processes, behaviour, motion capacity, and size. Combined, external and internal factors affect a frugivores' capacity as a seed disperser.

For zoochory to be effective, seed dispersal has to result in the recruitment of an adult plant. An important aim in the study of seed dispersal is to be able to understand and quantify the effects of zoochory on plant recruitment. Recent advances in seed dispersal ecology have led to the development and refining of a conceptual framework that considers the various quantitative and qualitative components that can influence the effectiveness of frugivores in dispersing seeds and the probability of plant establishment; the seed dispersal effectiveness conceptual framework (SDE; Schupp 1993; Schupp et al. 2010). The quantitative aspects of the SDE framework deal with the number of seeds dispersed by the frugivores (as a product of the visitation frequency and number of dispersed seeds

per visit), while the qualitative aspects consider the quality of treatment (e.g., effects of fruit handling and gut passage) and the quality of seed deposition (e.g., seeds dispersed to favourable microhabitats; Fig. 2).

The pairwise interactions between plants and frugivores do not occur in a vacuum, but are embedded in the ecological network of seed dispersal interactions between all plant species and all frugivores in the community (Bascompte & Jordano 2007). Therefore, if we want a deep understanding of the relative importance of chelonians as seed dispersers, we must look at their role in a community context. One of the factors that limit a detailed understanding of seed dispersal ecology is the complexity that arises in terms of the number of interspecific interactions, especially in species-rich ecosystems. This, in turn, limits our ability to address broad-scale questions and to reliably predict the outcomes of zoochory.

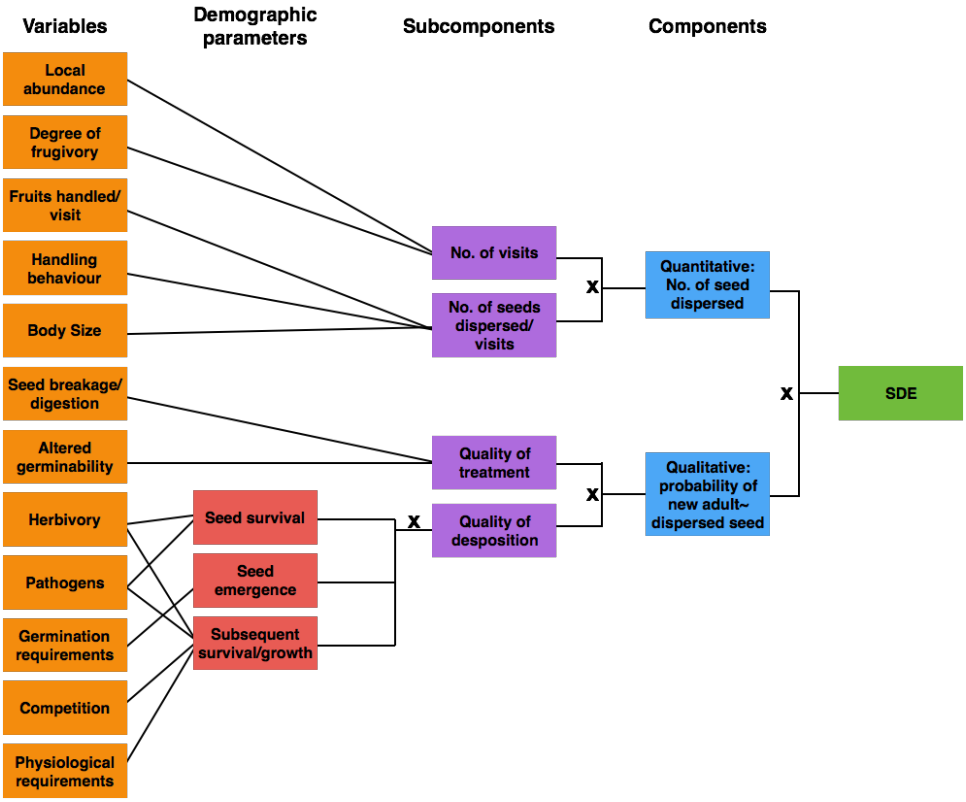

Figure 2: Hierarchical flowchart depicting the determinants that make-up the components of seed dispersal effectiveness (SDE) for endozoochory. Figure modified from Schupp et al. (2010).

Recent developments and applications of network theory to the study of mutualistic interactions have helped advance our understanding of the ecological processes driving zoochory (e.g., Bascompte & Jordano 2007; Bascompte et al. 2003;

Olesen et al. 2007). For example, the latter studies show that mutualistic networks are highly heterogeneous, with most species having relatively few interactions, while a few are more connected than expected by chance. This leads to networks having a nested structure, in which specialists interact with a subset of the species interacting with generalist ones. They have also shown that, depending on their size, networks can exhibit modularity, which is the presence of compartments with species that interact more frequently with each other while scantly interacting with species in other compartments. Furthermore, they indicate that the structure of mutualistic networks plays a significant role for species coexistence and stability, as well as for co-evolutionary processes.

One of the first modern FSD studies was Rick & Bowman's (1961) classic paper on how germination of an endemic Galápagos tomato was dramatically improved by passing through the gut of the endemic giant tortoises. It is ironic that chelonian FSD since then has progressed very little, despite several calls for studies of chelonians as seed dispersers (e.g., Moll & Jansen 1995; Pérez-Emán & Paolillo 1997).

In my thesis, I assessed the role of chelonians as seed dispersers, from species- to community level. I began by performing a review and synthesis of published and unpublished records of chelonian frugivory and seed dispersal in **Chapter 1**, where I focus on: i) the taxonomic and geographic distribution of chelonian FSD, ii) the taxonomical distribution and traits of plants dispersed by chelonians, and iii) chelonian SDE.

In the rest of my thesis, I focus on Aldabra giant tortoises (*Aldabrachelys gigantea*) on Aldabra Atoll to assess their role as frugivores and seed dispersers, and some of the factors that affect their capability as seed dispersers. As Sir David Attenborough put it, Aldabra Atoll is “one of the wonders of the world”, and was almost lost to military development, but thanks to the actions of scientists and conservationists the atoll was saved from certain destruction. Aldabra Atoll, in the southwestern Indian Ocean, has a land area of 155 km^2, and consists of four major islands (Fig. 3). Aldabra is a tropical atoll, with year-round high temperatures (mean range: 24–28˚C), and 975 mm of mean annual rainfall (Shekeine et al. 2015). The

atoll has a pronounced seasonality in precipitation, with a wet season from November–April, and a dry season from May–October. The dominant terrestrial habitat types on the atoll are standard mixed scrub (43.3 km^2), followed by pemphis scrub (35.8 km^2), open mixed scrub (25.4 km^2), and grassland (4.5 km^2; Walton et al. in review). Different from other islands in the Indian Ocean, Aldabra supports an almost intact native fauna and flora, with very few invasive species (e.g., rats, cats) on some islands. Reflecting its uniqueness, Aldabra was declared a UNESCO World Heritage Site in 1982.

Figure 3: Map of Aldabra Atoll, Seychelles, in the western Indian Ocean. Map obtained from, and used with the permission of Save our Seas Foundation.

Compared to other ecosystems whose seed dispersal networks have been studied (e.g., Canary Islands, Gonzalez-Castro et al. 2012; Pantanal, Donatti et al. 2011), Aldabra is a very recently assembled ecosystem, where there has been comparatively little time for co-evolution of traits between fruits and frugivores. The atoll is therefore also of paramount interest as a system in which we can progress our understanding of the assembly of ecological networks, a much-vaunted goal in ecology (Bascompte & Stouffer 2009).

The potential vertebrate frugivore guild of Aldabra is small but highly diverse, comprising a total of 15 species of birds, mammals, reptiles, and terrestrial crabs.

There are 51 fleshy-fruited plant species belonging to 36 families on the atoll (ca. 40% of Aldabra's flora, *sensu* Fosberg & Renvoize 1980; excluding grasses and sedges). Most importantly, Aldabra is one of the very few ecosystems in the world that still has its full size-range of frugivores, from the megafaunal tortoise to the very small gecko and passerines.

Figure 4: An Aldabra giant tortoise (*Aldabrachelys gigantea*) from East Grande Terre, Aldabra Atoll, Seychelles.

Amongst the frugivores on Aldabra, perhaps the most notable one is the megafaunal Aldabra giant tortoise (*Aldabrachelys gigantea*; Fig. 4). Aldabra Atoll is the last bastion of giant tortoises in the Indian Ocean, with the only other extant giant being the Galápagos giant tortoise (*Chelonoidis nigra*). Evidence is mounting that tortoises are important but overlooked seed dispersers in ecosystems ranging from coastal shrub and dry deserts to rainforests, and from continents to islands (Heleno et al. 2011; Jerozolimski et al. 2009; Strong & Fragoso 2006; Varela & Bucher 2002). Nevertheless, it is especially on islands, where giant tortoises often are –or were– the largest vertebrate megafauna (Hansen & Galetti 2009; Hansen et al. 2010), that we find the strongest evidence of tortoises as major seed dispersers (Blake et al. 2012; Hansen et al. 2008; Heleno et al. 2011; Hnatiuk 1978; Rick &

Bowman 1961). Moreover, tortoises can be considered ecosystem engineers because they heavily influence many ecosystem dynamics, such as herbivory, nutrient cycling, and the creation and maintenance of habitat heterogeneity (e.g., via trampling or digging; Hansen et al. 2010, and references therein). This, together with the fact that Aldabra is the last place on Earth where giant tortoises –a group of formerly widespread, major seed dispersers– can be studied in virtually pristine conditions, provides the motivation for the focus on Aldabra giant tortoises as the likely main drivers of the seed dispersal network on Aldabra. Therefore, the focal frugivore of my thesis are Aldabra giant tortoises, which are giants that weigh up to 150 kg (in the wild).

In **Chapter 2**, I assessed the role of Aldabra giant tortoises in the seed dispersal community of Aldabra Atoll in relation to other frugivores. Moreover, in **Chapter 3**, I also examined whether tortoise size and/or seed size affect their gut retention times. Finally, I studied the thermoregulatory ecology of giant tortoises in **Chapter 4**, and looked at how environmental temperature affect their activity and body temperature (and potentially their role as seed dispersers). I then applied the findings about their thermoregulatory environment in the wild to the management and husbandry of captive tortoises in **Chapter 5**.

I wrote all the chapters as independent manuscripts for papers. Consequently, there is substantial overlap between some sections of some chapters. However, rather than annoying the reader too much, this will hopefully reinforce two main points. Firstly, the notion that chelonians are important frugivores and seed dispersers. Secondly, that Aldabra giant tortoises, in particular, are important functional megafaunal frugivores and seed dispersers.

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1

FRUGIVORY AND SEED DISPERSAL BY CHELONIANS: A REVIEW AND SYNTHESIS

CHAPTER 1

Frugivory and seed dispersal by chelonians: A review and synthesis

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Abstract

In recent years, it has become clear that frugivory and seed dispersal (FSD) by turtles and tortoises is much more common than previously thought. Yet, a review and synthesis is lacking. We here review published and unpublished records of chelonian FSD, and assess their role as seed dispersers, from individual species to the community level. We first discuss the distribution of chelonian FSD, and the characteristics of the fruit and/or seed species eaten and dispersed by chelonians. We then use the seed dispersal efficiency framework to explore the quantitative and qualitative components of seed dispersal by tortoises and turtles, embarking on a journey from when the fruits and/or seeds are consumed, to when and where they are deposited, and assessing how efficient chelonians are as seed dispersers. We finally proceed to discuss chelonian FSD in the context of communities and as megafauna. A substantial proportion of the world's aquatic and terrestrial turtles and a major part of testudinid tortoises (70 species in 12 families) include fruits and/or seeds in the diet that span at least 588 plant species in 120 families. For some species, overall or in certain seasons, fruit may even form the largest part of their diet. Most importantly, contrary to the other major reptilian seed dispersers, lizards, chelonian FSD is not an island phenomenon in terms of geographic distribution. Nevertheless, on islands especially tortoises are often among the largest native terrestrial vertebrates—or were, until humans got there. We synthesize the lessons learned so far in terms of chelonian FSD, and discuss the relevance of our findings for conservation and restoration, especially in relation to rewilding with large and giant tortoises.

Keywords: *Angiosperms, Testudines, tortoises, turtles, plant–animal interactions*

Resumen

En años recientes, se ha hecho claro que la frugivoría y dispersión de semillas (FDS) llevada a cabo por tortugas (quelónidos) es más común de lo antes pensado. No obstante, todavía carecemos de una revisión y síntesis sobre este tema. En este artículo, revisamos récords (publicados y no publicados) sobre FDS por quelónidos, y evaluamos su rol como dispersores de semillas, desde el nivel de individuos, al nivel de comunidades. Primero, discutimos la distribución de FDS por quelónidos, y las características de las especies de frutos y/o semillas consumidas y dispersadas por tortugas. Luego hacemos uso del concepto de la eficiencia de dispersión de semillas como marco de referencia para explorar los componentes cualitativos y cuantitativos de la FDS por quelónidos, embarcándonos en un viaje desde cuando los frutos y/o semillas son consumidas, hasta cuando son depositadas. También evaluamos cuán eficientes son los quelónidos como dispersores de semillas. Finalmente procedemos a discutir la FDS por quelónidos en el contexto de comunidades, y como 'megafauna'. Una proporción substancial de las tortugas acuáticas del mundo y la mayor parte de las tortugas testudínidas (70 especies en 12 familias) incluyen frutos y/o semillas en su dieta que abarcan al menos 588 especies de plantas en 120 familias. En algunas especies, en general o en algunas estaciones, la mayor parte de su dieta está conformada por frutas y/o semillas. Más importante aún, y contrario a las lagartijas, que son otro grupo importante de reptiles que incurre en FDS, la frugivoría y dispersión de semillas por quelónidos no es un fenómeno de islas solamente, en términos de distribución geográfica. Empero, en islas, especialmente las tortugas terrestres, están entre los vertebrados nativos de mayor tamaño–o lo estuvieron, hasta que los humanos llegaron a ellas. En este artículo, hacemos una síntesis de las lecciones aprendidas hasta ahora sobre la FDS por quelónidos, y discutimos la relevancia de nuestros hallazgos para la conservación y restauración, especialmente en relación a proyectos de resilvestrar ('rewilding') con tortugas gigantes o de gran tamaño.

Introduction

Animal-mediated seed dispersal is the process by which animals disperse the seeds away from the mother plant (Fig. 1), and is an important ecological function that has profound ecological and evolutionary implications in ecosystems (Howe & Smallwood 1982; Rezende et al. 2007; Stoner & Henry 2008). The distribution and ecology of frugivory and seed dispersal (FSD) in most major vertebrate taxa has been thoroughly investigated and results synthesised (Estrada & Fleming 1986; Levey et al. 2002), most recently for lizards (Iverson 1985; Olesen & Valido 2003; Valido & Olesen 2007; Whitaker 2011), and a start has even been made for crocodilians (Platt et al. 2013). However, a thorough overview and synthesis is still missing for chelonians.

Reviewing the origin and rise of frugivory and seed dispersal through deep time, Tiffney (2004) established that plants had the necessary morphological features for vertebrate dispersal by the Late Carboniferous (323.2–298.9 Ma), and that by the middle of the Mesozoic (252–66 Ma), several reptile lineages could have established specific FSD associations with plants. Given the long evolutionary history of chelonians, and the generally broad diet of many species alive today, we could expect that, chelonians were amongst the early frugivores and seed dispersers in evolutionary time. Indeed, chelonians have been suggested to be early dispersers and 'first movers' in the evolutionary ecology of fruits (Ridley 1930; Tiffney 1986; 2004; van der Pijl 1969). Perhaps the earliest example of frugivory by chelonians comes from a Campanian (83.6–72.1 Ma) coprolite that likely originated from a turtle, and that contained ca. 200 achenes of a Ranunculaceae sp. (Rodriguez-de la Rosa et al. 1998). Moreover, hackberry (*Celtis*, Cannabaceae) seeds were found inside two fossilised specimens of *Stylemys* tortoises in South Dakota from the Oligocene (33.9–23.03 Ma; Marron & Moore 2013). On the Bahamas, two out of three extremely well-preserved individual carapaces of the recently extinct (4,200–1,200 BP) giant tortoise (*Chelonoidis alburyorum*) contained many seeds of two large-fruited species (wild mastic, *Mastichodendron foetidissimum*, and satinleaf *Chrysophyllum oliviforme*; both Sapotaceae; Franz & Franz 2009; Steadman et al. 2007). In historical times, early settlers of the Mascarene Islands observed how now-extinct giant tortoises

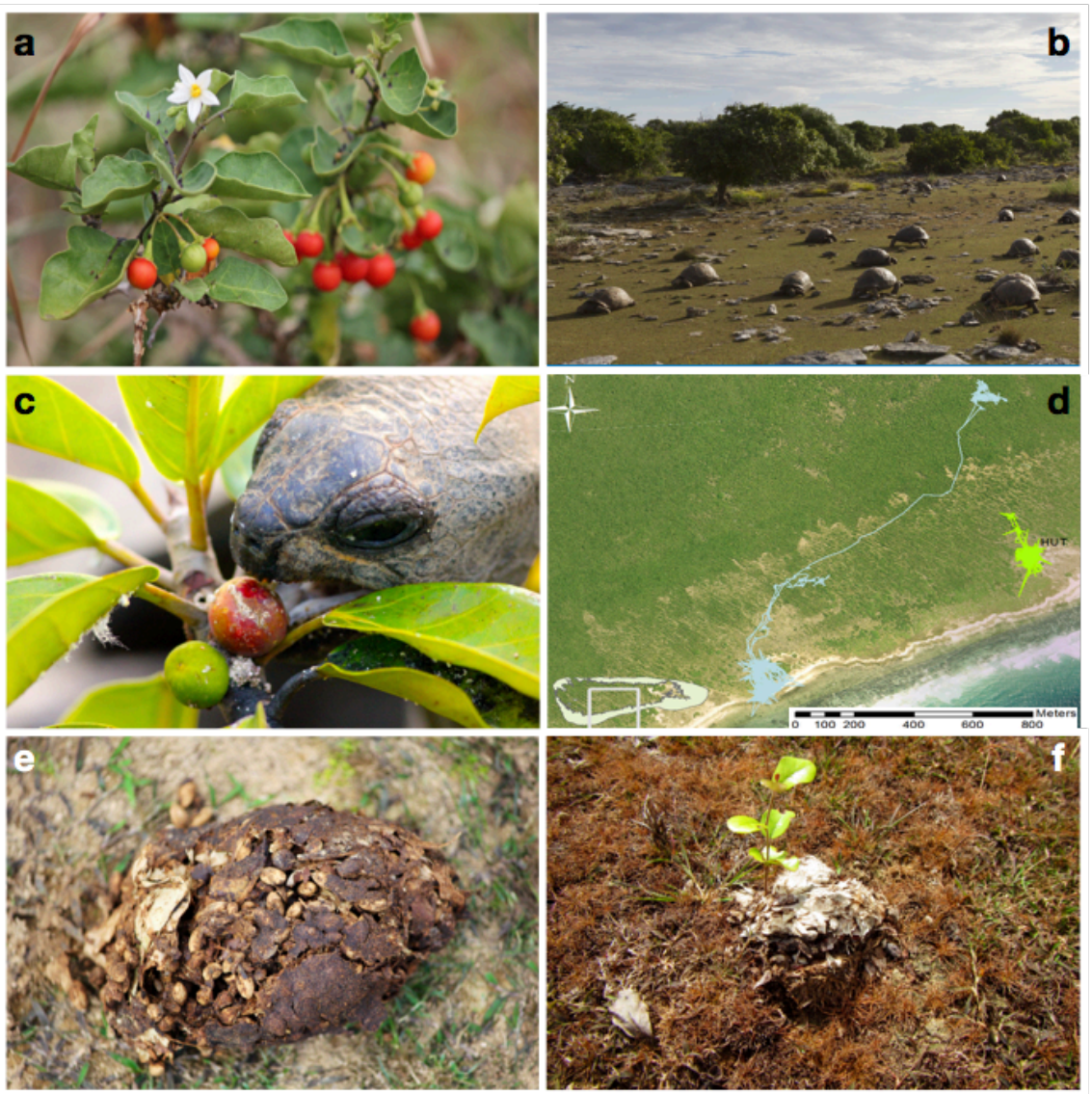

Figure 1: The process and outcome of chelonian-mediated seed dispersal, here exemplified by Aldabra giant tortoises (*Aldabrachelys gigantea*) on Aldabra Atoll, Seychelles. Fruiting plants like the Aldabra tomato (*Solanum aldabrense*) attract giant tortoises (a), which occur at high densities on the atoll (b). Fruits are a large component of the diet of giant tortoises, and they have often been observed eating ripe fruits, while ignoring green ones (e.g., of *Ficus nautarum*; c). After ingestion, seeds are retained for an average of 15 days in the guts of the tortoises; a time period during which tortoises can move considerable distances across the landscape (d; movement paths of two individuals on the south of the atoll). Once defecated, a single scat of giant tortoises can contain over 150 seeds, and often results in germination (e-f; seeds and a seedling of *Terminalia bovinii*).

(*Cylindraspis* spp.) included fruit in their diet. In Mauritius in the late 1600s the tortoises were reported to eat 'apples' (= endemic ebony *Diospyros*, Ebenaceae, and Sapotaceae fruits; Hume & Winters 2016). On nearby Rodrigues Island, the exiled French Huguenot François Leguat and his men ate many fruits from the forest, but

"left the dates [= palm fruits, Arecaceae] for the turtles [= giant tortoises, *Cylindraspis* spp.]" (Leguat 1708).

One of the first modern, experimental FSD studies was Rick & Bowman's (1961) classic paper on how the germination rate of an endemic Galápagos tomato was dramatically improved by passing through the gut of the endemic giant tortoises. It is ironic that, despite several calls for studies of turtles as seed dispersers (e.g., Moll & Jansen 1995; Pérez-Emán & Paolillo 1997), our understanding of chelonian FSD has progressed very little since then. In this review, we aim to summarise published and unpublished information about chelonian FSD in the wild, and synthesise and discuss the role of chelonians as frugivores and seed dispersers. We first present an overview of the taxonomical distribution of chelonian FSD, as well as of the taxonomical distribution of plants consumed by chelonians. We then use the concept of seed dispersal effectiveness (SDE; Schupp 1993; Schupp et al. 2010) to discuss the quantitative and qualitative aspects of chelonian seed dispersal. We progress to discuss the role of chelonians in the FSD community, as megafaunal seed dispersers, and their role in conservation and restoration efforts.

Methods and data

To synthesise data on FSD by chelonians, we performed a comprehensive literature search that included scientific articles, books, monographs, and theses. We used Google Scholar (http://scholar.google.com/), as it has been found to include and exceed the results of other commonly used literature databases (specifically WoS and Scopus; see Svenning et al. 2016). We used the following search terms: 'diet', 'frugivory', 'seed dispersal', in combination with the Latin genera of chelonians (from van Dijk et al. 2014), or the keywords 'chelonian', 'tortoise', or 'turtle'. No constraints on the year of publication or language were imposed (i.e., we found some articles in other languages, e.g., Spanish). We filtered the search results by reading the abstracts, and going through the references of each text found to identify other potentially suitable articles. We added literature known by the authors to include diet information, but which did not appear in our search (mostly books). In addition, we added unpublished data based on our observations and shared by various researchers. For diet data, we only included information based on wild

chelonians. For germination and gut passage experiments, we included studies using captive chelonians conducted with fruits found in the natural habitat of the species. To give a more complete overview of some of the main variables that determine the outcome of seed dispersal, we reviewed information on gut retention time (GRT), and on movement ecology and habitat range of chelonians. We used the same approach as above, using each of the search terms, 'gut retention time', 'movement', 'activity' and 'home range' together with 'tortoise', 'turtle' or 'chelonian'. See Appendix 1 for the resulting reference lists.

We followed van Dijk et al. (2014) for chelonian taxonomy, and the iPlant Collaborative for plant taxonomy (Boyle et al. 2013; http://tnrs.iplantcollaborative.org/). For data on chelonian body mass, we used the amniote life-history database (Myhrvold et al. 2015). When studies only showed results graphically, we extracted the data from figures using WebPlotDigitizer ver. 4.0 (Rohatgi 2017; https://automeris.io/WebPlotDigitizer/). We analysed and visualised the data using R v. 3.3.3 (R Core Team 2017) and the package 'ggplot2' (Wickham 2016).

Overall, we were able to extract data from 167 studies on chelonian FSD, germination, GRT, and movement. We found 106 studies containing data on FSD by wild chelonians. These arose from either focused FSD studies (i.e., studies focusing directly on the role of chelonians as frugivores and/or seed dispersers; n = 24), partial FSD studies (i.e., studies that examine diet in relation to/in a framing of FSD or examine gut passage, but not germination; n = 70), or diet studies (not framed in an FSD context; n = 12). The studies used several methods to obtain data on FSD by chelonians, including direct observation, camera traps (e.g., Wang et al. 2011), stomach flushing (e.g., Legler 1977), or analysis of collected faeces (e.g., Nogales et al. 2017). Faecal collection methods ranged from simple picking up, to more creative approaches, such as collection with a miniature wheeled barrow mounted behind the animal (Josseaume 2002), and, for marine turtles, collecting in cloaca-mounted bags (Amorocho & Reina 2008). Determination of the seed content in the faeces was done with either direct counts of seeds, or counting any seeds that germinated from the dung (e.g., Hnatiuk 1978). For chelonian GRT, we found 37 studies, which were

conducted by feeding fruits and/or artificial particles. Finally, we found 24 studies on chelonian movement and home ranges.

There are inherent biases associated with the different methodologies when estimating chelonian FSD. In dietary studies, seeds might often be overlooked, or underreported/not specifically mentioned as plant diet components. For example, Mouden et al. (2006) have a long list of plants recorded in the spur-thighed tortoise (*Testudo graeca*) scat, many, but not all of which, overlap with those of Cobo & Andreu (1988), who specifically studied seeds dispersed by *T. graeca*. Also, Kabigumila (2001) and Hansen et al. (1976) provide a long list of food plants in the scat of the leopard tortoise (*Stigmochelys pardalis*) and the Mojave desert tortoise (*Gopherus agassizii*), respectively, but they did not specify whether these were fruits, seeds or other plant parts. In addition, faecal analysis alone may provide a biased account of a species' diet. For example, de Lima et al. (1997) describe the red side-necked turtle (*Rhinemys rufipes*) as a major frugivore "palm specialist" based on faecal analysis, but a subsequent study by Caputo & Vogt (2008), using stomach flushes, found relatively larger amounts of animal food items. Thus, faecal analysis tends to record more plant matter, while it can grossly underrepresent the importance of animal matter in the diet (Caputo & Vogt 2008). Moreover, stomach flushing may underestimate frugivory, as large seeds are hard to dislodge (de Lima et al. 1997; Kennett & Tory 1996). Another aspect that can bias the available data is the seasonality in the diet of some chelonians, where fruit may only be a major part of the diet in some season(s). Short-term studies that don't span different seasons may underestimate fruit consumption and thus the potential for seed dispersal. This is important if we take into consideration that only 9% of the studies considered seasonality in the diet of chelonians. All these factors underscore the need for comprehensive dietary sampling when considering the feeding type of chelonians and their role as frugivores and seed dispersers.

Distribution of chelonian FSD

Taxonomical distribution

Chelonians comprise about 335 species, of which 275 are turtles and 60 are tortoises, spanning 94 genera in 14 families (van Dijk et al. 2014). We found a total of

72 species that engaged in FSD, distributed across all major chelonian phylogenetic groups (Fig. 2), except for Dermochelyidae (with the marine leatherback turtle, *Dermochelys coriacea*, as the only extant species).

There was a notable gap in FSD in the branches containing *Platemys platychephala* to *Acanthochelys* spp. (tree 1 in Fig. 2, from left to right; Chelidae), *Pelochelys* spp. and *Chitra* spp. (tree 2; Trionichydae), and containing from *Orlitia borneensis* to *Pangshura smithii* (tree 3; Geomydidae). However, FSD was recorded in other species within these three families. This pattern is likely due to the lack of focused dietary or FSD studies on these species. Moreover, as we will see below, habitat and seasonal influences on the diet of these groups may influence the levels of FSD in different locations and times of the year, therefore affecting sampling results. The few other chelonian species without any reported FSD have been described as purely carnivorous. Thus, frugivory is widespread in Testudines, with most taxa having at least one frugivorous representative at the genus level.

Geographical distribution

Chelonians are widely distributed across the world, inhabiting habitats from tropical to temperate, from continents to islands and oceans, and they include terrestrial, aquatic and semi-aquatic, as well as marine species (see van Dijk et al. 2014 for individual species distributions). Chelonian species richness peaks in the south-eastern USA, the Ganges Delta, Southeast Asia, and northern South America (Fig. 3a; Roll et al. 2017). Furthermore, the geographic distribution of species richness of chelonian species that engage in FSD is concentrated in the south-eastern USA and northern South America, highlighting the underrepresentation of studies for especially south-east Asia (Fig 3b). Thus, unlike FSD by lizards (Olesen & Valido 2003), FSD by chelonians is not restricted to islands, and they can thus potentially play a major role in continental and island ecosystems alike.

Figure 4 shows the eight most fruit-loving chelonians, of which seven are Testudinid species and one species in the Emydidae.

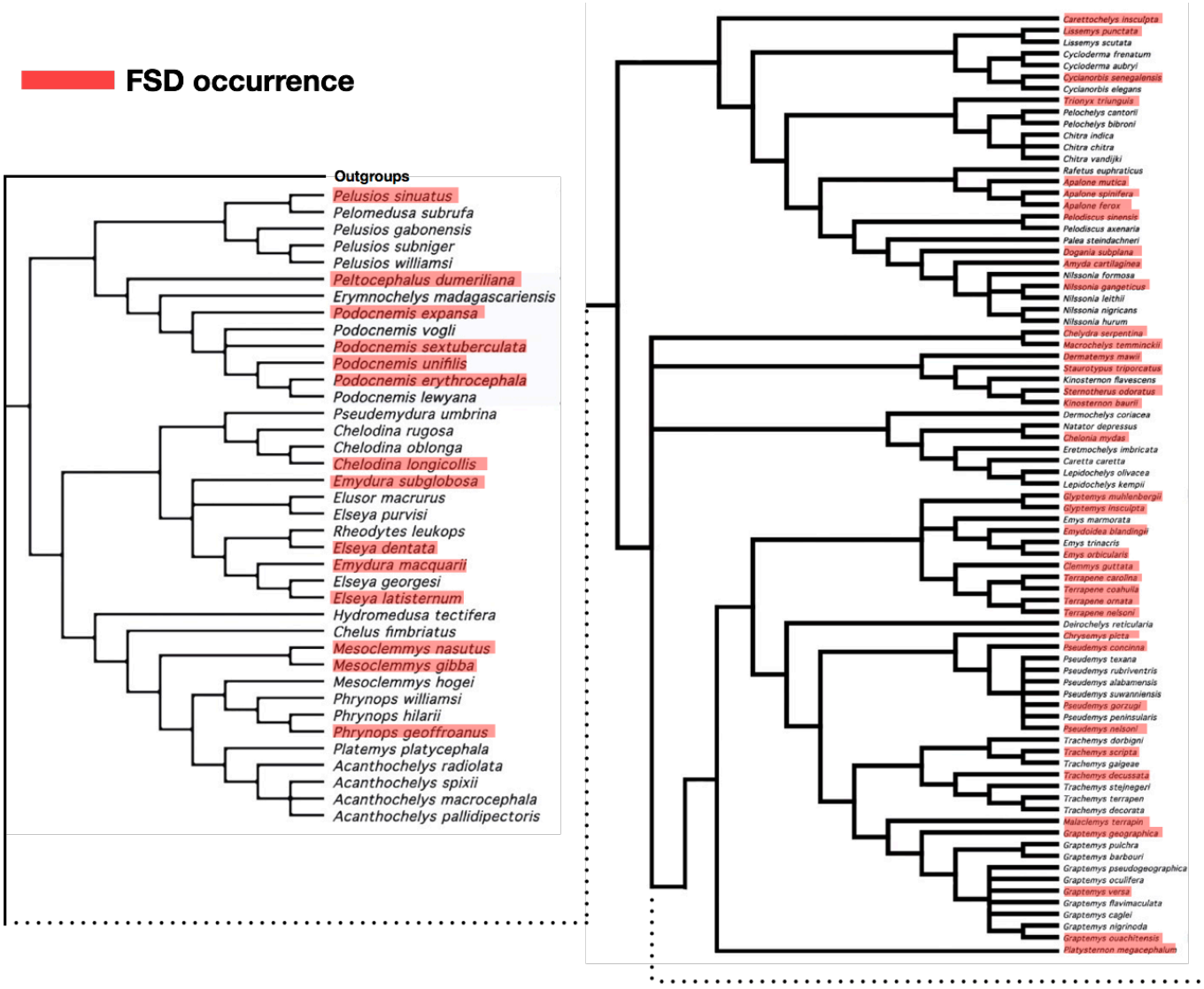

Figure 2: Taxonomical distribution of frugivory and seed dispersal in chelonians. Red shading denotes occurrence of frugivory and seed dispersal in each. Figure modified from Guillon *et al.* 2012. Note that not all chelonian species that engage in FSD are present in the phylogeny.

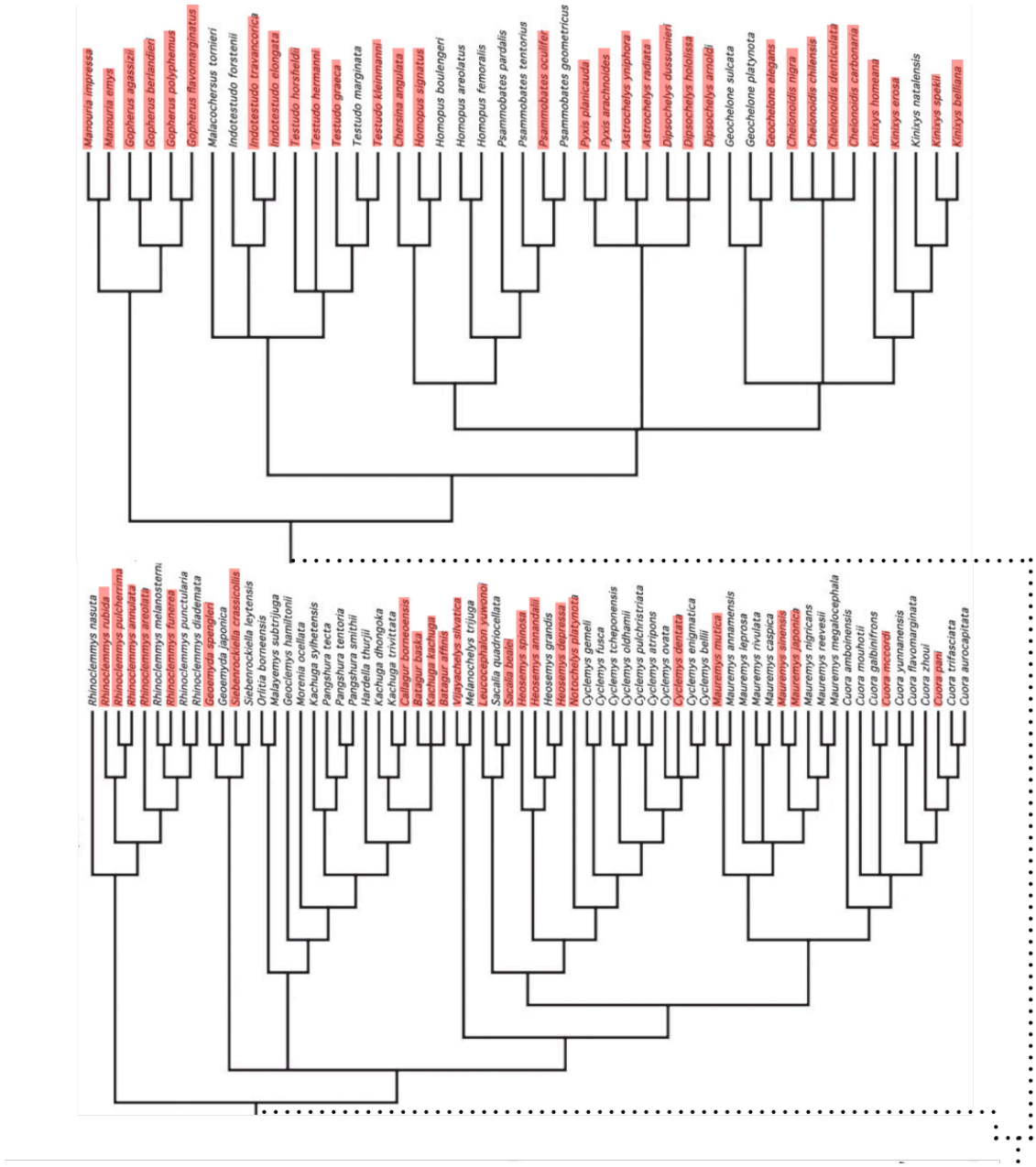

Figure 2: Cont.

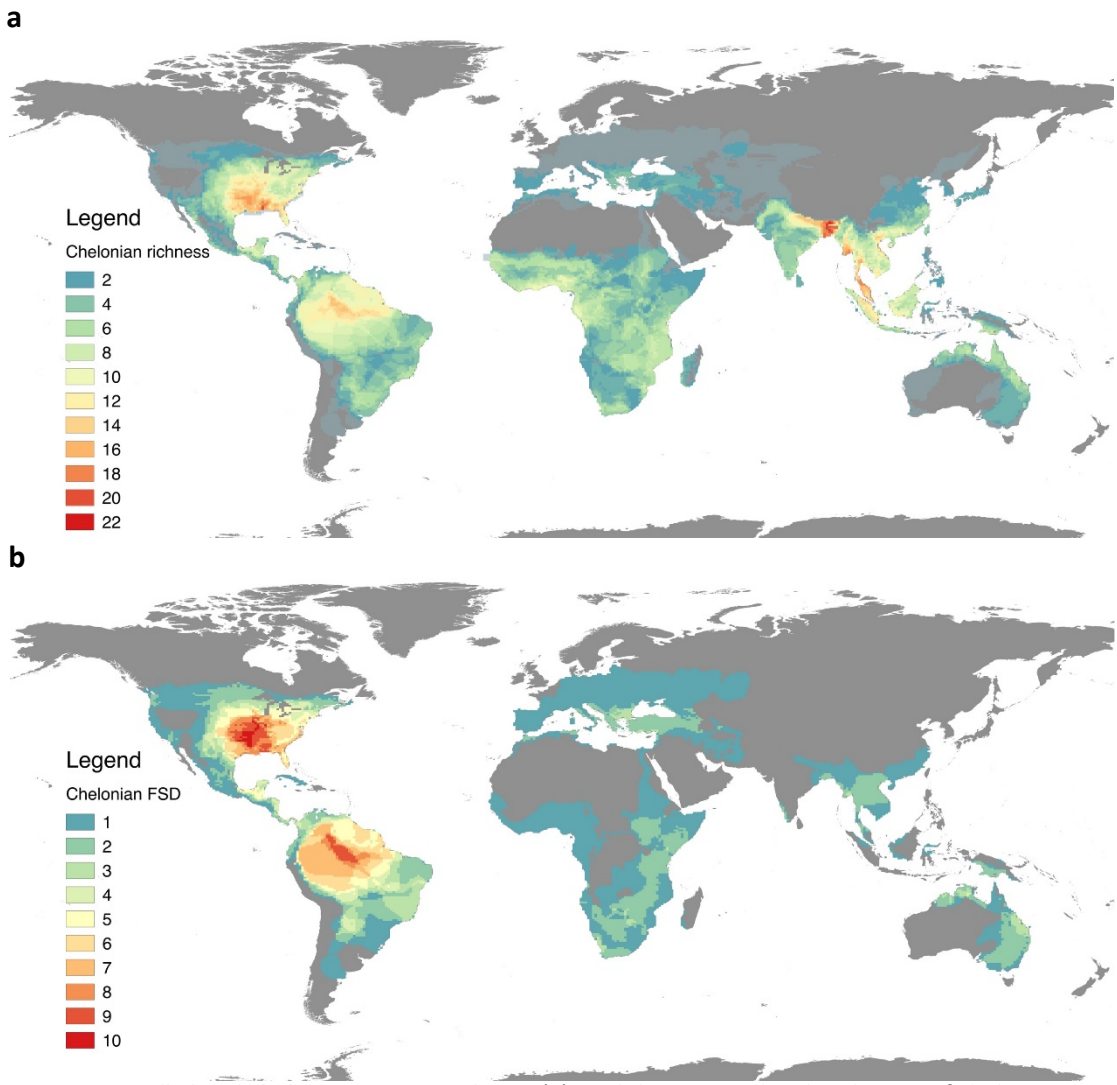

Figure 3: Overall global chelonian species richness (a), and the geographic distribution of chelonians for which we found records of frugivory and/or seed dispersal (b), excluding marine species. Note the difference in magnitude in the colour gradients of the legend. Data from Roll et al. (2017), provided by Y. Itescu.

Figure 4: The most fruit-loving chelonians, with the number of fruit species consumed by each chelonian species indicatd below. Notice that seven of these are tortoises (Testudinidae), with *T. carolina* belonging to the Emydidae.

Patterns of generalisation and specialisation

Specialisation or generalisation on fruits varies depending on the chelonian species as expected by the different main feeding types (herbivores, carnivores or omnivores). Frugivorous tortoises can vary from generalist, specialist to opportunistic frugivores. For example, *Chelonoidis* tortoises in South America are generalist frugivores, consuming fruits having a variety of traits (Guzmán & Stevenson 2008; Moskovits 1985). At the opposite end of the spectrum, we have highly specialised Gibba turtle (*Mesoclemys gibba* [*Phrynops gibbus*]) that feeds almost exclusively on palm fruits (*Mauritia flexuosa*, Aracaceae) during part of the year in the Rio Negro Basin in Brazil (RC Vogt, pers. comm.). Other species such as the common snapping turtle (*Chelydra serpentina*) are omnivorous, incorporating roughly the same amount of plant material (including fruits) and animal material in their diet (Ernst & Lovich 2009). Lastly, there are species that are mostly carnivorous, which will eat fruits opportunistically, such as Blanding's turtle (*Emydoidea blandingi*; Rowe 1992) and hinge-back tortoises (*Kinixys* spp.; Luiselli 2003). Most frugivorous chelonian species are generalist frugivores that also include other plant material in their diet; this is especially true for tortoises (Testudinidae).

Functional traits in relation to FSD

Frugivore species have inter- and intraspecific differences in functional traits, which may result in large differences in the seed dispersal services they provide (Jordano et al. 2007; Zwolak 2017). For example, differences in habits, size and age, sex, cognition and preferences. Knowledge about these traits will help us understand the role of specific characteristics of frugivores in their effectiveness as seed dispersers.

Habitat–. Chelonians are a diverse group of vertebrates whose different habits, such as terrestrial, semi-aquatic, aquatic and marine, have allowed them to exploit many habitats and resources. Terrestrial plants and tortoises are perhaps the first that come to mind when thinking about seed dispersal in this group. Terrestrial plants can be considered more zoochorous than their aquatic counterparts, and because of their habitat, tortoises and terrestrial –or semi-aquatic– turtles are more likely to encounter fruits and disperse their seeds within terrestrial habitats.

However, as we found, seed dispersal is also carried out by mainly aquatic species, both on land and in water, for terrestrial and aquatic plants, and even for coastal and marine plants in marine ecosystems. Yet, despite the early mention of the role of both terrestrial (Rick & Bowman 1961) and aquatic species (Kennett & Russell-Smith 1993), most studies of chelonian FSD have focused on terrestrial chelonians, largely ignoring the role of aquatic and marine species in seed dispersal (Moll and Jansen 1995). Ultimately, the habitats of both chelonians and of the plants they encounter, will determine which fruits are available to each species, and whereto the seeds can be dispersed.

Size and age–. Tortoises and turtles exhibit great inter- and intraspecific size variation. Size increases with age in chelonians (Waibel et al. 2013). From the perspective of FSD, the size of chelonians limits the size and the number of fruits and/or seeds they can swallow and pass through their guts. Furthermore, size may affect gut passage time (see section on mouth and gut passage treatment) and volume of the scat. Thus, size is expected to substantially affect the ability and effectiveness of chelonians as seed dispersers (see also section on chelonians as megafaunal seed dispersers).

Ontogenetic changes in diet may also occur in chelonians, with vegetation becoming more important as chelonians age and become larger (Moll 1976); this seems to be common in omnivorous turtles (Clark & Gibbons 1969; Georges 1982; Hart 1983; Sung et al. 2016). In the case of the omnivorous red side-necked turtle (*Rhinemys (Phrynops) rufipes*), de Lima et al. (1997) found that most of the scat volume was palm seeds, and that the frequency of palm seeds increased with turtle size. These ontogenetic changes in diet may be accompanied by changes in gut morphology, as found in the green sea turtle (*Chelonia mydas*), with long to short intestine ratios increasing from 0.45 in post-hatchlings to 2.5 in adults, which might reflect a higher proportion of animal matter in the diets of young individuals (Davenport et al. 1989).

Sex–. Sexual dimorphism is common in this group, but the direction of sexual dimorphism depends on the species and even on habitat. For example, males of

angulate tortoises (*Chersina angulata*) are larger than females, whereas females of leopard tortoises (*Stigmochelys pardalis*) tortoises are larger than males within the same habitat (Mason et al. 2000). In the case of Aldabra giant tortoises (*Aldabrachelys gigantea*), the population exhibits no sexual dimorphism on the east of Aldabra Atoll, but males gradually attain larger sizes compared to females towards the western side of the atoll (Turnbull et al. 2015). As described above, size is expected to have a differential effect on seed dispersal, and there may thus be differences in the seed dispersal provided by males and females. For example, where sexual dimorphism is present, the larger males of Aldabra giant tortoises are able to extend their necks to reach higher vegetation and fruits than the smaller females can (WF & DMH, pers. obs). Males and females may also exhibit different behaviours, e.g., habitat selection, which can affect the outcome of FSD. For example, most of the stomach contents of the omnivorous female smooth softshell turtle (*Apalone mutica*) were aquatic items, whereas stomach content of males was mostly terrestrial items and included more fruits (Plummer & Farrar 1981). These sexual differences in terms of diet were attributed to the different microhabitat preferences (females forage in deep water, whereas males forage in the interface between aquatic and terrestrial habitats). Furthermore, males and females of some species may show differences in home range size and displacement distances (see below). Difference in habitat selection, home range size and displacement distances are not only expected to affect the ability of chelonians to exploit fruits, but also their effectiveness as seed dispersers.

Cognition and behaviour–. Chelonians, as other animals, rely on cognitive processes to acquire knowledge about their environment through their senses, leading to learning and memory creation. The sensory features of fruits play an important role in attracting frugivorous birds and aid in their selection (Schaefer et al. 2008b), and this is expected to be the case for chelonians as well. Sight and olfaction are the sensory faculties that aid turtles and tortoises in the recognition of food sources. Chelonians can perceive images and distinguish colours in the human-visible spectrum (Ammermüller et al. 1995; Arnold & Neumeyer 1987; Baylor & Fettitplace 1975; Granda & Stirling 1965; Mathger et al. 2007; Neumeyer & Jäger 1985; Pellitteri-Rosa et al. 2010; Schwartz 1975; Twig & Perlman 2004; Ventura et al.

2001), and some have been shown to also have sensitivity to the ultraviolet spectrum (Ammermüller et al. 1998; Ventura et al. 1999; Zana et al. 2001). Additionally, chelonians have a highly developed olfactory (vomeronasal) system (Fadool et al. 2001; Manteifel et al. 1992; Murphy et al. 2001), which they can use to detect volatile chemicals excreted by plants from long distances (King 1996), and also to smell fruits at close range, possibly to evaluate ripeness (WF, DMH, DM, pers. obs.).

Learning and memory of frugivores has an important impact on seed dispersal, because decision-making based on previous experiences can determine which plants and which fruits are selected and consumed, and ultimately where seeds are dispersed (reviewed in John et al. 2016). A model by John et al. (2016) testing frugivores with different spatial memory skills suggested that those with longer spatial memory are able to relocate food sources more efficiently, survive longer and disperse larger amounts of seeds. They also moved less at random around the landscape, which led to differences in terms of the spatial distribution of seeds dispersed compared to animals with shorter memory. Captive red-footed tortoises (*Chelonoidis carbonaria*) can navigate efficiently in their environment, and they can remember spatial location of food for at least two months (Soldati 2015). Moreover, they were able to anticipate food availability over periods of 24 h, discriminating between the quality and quantity of food, and remembering these attributes for at least 18 months. In relation to large-scale movement patterns, individuals of both Galápagos (Blake et al. 2013) and Aldabra giant tortoises (Baxter 2015) have been shown to follow the same movement patterns in different years, implying that they have a persistent spatial memory.

Chelonians may use landmarks and different stimuli to orient themselves and find suitable food sources. For example, sulcata tortoises (*Geochelone sulcata*) and leopard tortoises (*Stigmochelys pardalis*) have been shown to discriminate between colours and shapes, and associate these features with navigation to food sources when tested on a T-maze (Janisch 2013). Moreover, the red-footed tortoises can navigate between known localities where fallen fruits are available at certain seasons (Josseaume 2002). Also, fallen fruits encountered are often from foraging activity of arboreal/aerial frugivores (Moll & Jansen 1995), and it is thus possible that

chelonians can use cues from other species to find food. This seems to be the case in in Malaysia, where painted terrapins (*Batagur borneoensis*) have been observed clustering in the water under a troop of leaf monkeys in trees above to eat berembang fruits (*Sonneratia caseolaris*, Lythraceae) that the monkeys were throwing into the water (Moll 1980b).

By navigating the landscape based on previous experiences, chelonians can identify and exploit fruits. For example, Legler (1976) noted that the northern snapping turtle (*Elseya dentata*) in Australia exploits windfall fruits of fig trees, with large congregations of these turtles found around this resource. In addition, other aquatic species such as the black river turtle (*Rhinoclemmys funerea;* Moll & Jansen 1995) and the Central American river turtle (*Dermatemys mawii;* Moll 1989) have been observed clustering and waiting in water beneath fruiting *Ficus glabrata* (Moraceae) trees, and the painted terrapin (*Batagur (Callagur) borneoensis*) displays similar clustering in the water under berembeng trees with falling fruits in Malaysian rivers (Moll 1980b). Similarly, the Travancore tortoise in India (*Indotestudo travancoria*; Bonin et al. 2006; Kanagavel & Raghavan 2012), and in Brazil, the red-footed tortoise (*Chelonoidis carbonaria*; Moskovits & Bjorndal 1990) congregate beneath favoured fruiting trees to exploit these food resources. Notably, the tree *Spondias testudinis* (Anacardiaceae) was named for the yellow-footed tortoises (*C. denticulata*; Mitchell & Daly 1998) that flock beneath fruiting trees to feed on the large, yellow-brown fruits (D Daly, pers. comm.). Furthermore, aquatic Antillean sliders (*Trachemys decussata*) in Cuba will emerge onto the land in great numbers after rains to feed on fallen jobo (*Spondias lutea*) and Bagá (*Anona palustris,* Annonaceae) fruits that have fallen from riparian trees (Barbour & Carr 1940). Thus, chelonians possess landscape-scale spatial awareness of food (fruit/seed)-plants.

Fruit preferences–. Animals rely on their ability to detect differences in food quality by using sensory adaptations, which allows them to circumvent some of the costs associated with foraging (Borges et al. 2011). Frugivores can establish and maintain preferences based on colour, odour and taste (Levey 1987; Sorensen 1983; Willson & Comet 1993; Willson et al. 1990). As discussed above, chelonians have highly developed visual and olfactory systems, and are known to be attracted by

smell and colour (see Harless & Morlock 1979 for a review), which may lead to the establishment of preferences. Indeed, studies focusing on colour preferences in tortoises have found preferences for distinct visual stimuli. For example, probably the first study that explored colour preferences in chelonians was done by Grant (1960) on Texas tortoises (*Gopherus berlandieri*), which exhibited a strong preference for red, selecting food items dyed red after having initially rejected them (i.e., when the same food items had other colours). Subsequent studies using spur-thighed tortoises (*Testudo graeca*; Pellitteri-Rosa et al. 2010), yellow-footed tortoises (*Chelonoidis denticulata*; Passos et al. 2014) and Aldabra giant tortoises (*Aldabrachelys gigantea*; Spiezio et al. 2017; DMH, unpubl.) have shown a prevalent preference for yellow, and/or red colours. Furthermore, chelonians have been shown to discriminate between odours to identify potential mates and conspecifics (e.g., Auffenberg 1965; Galeotti et al. 2009; Polo-Cavia et al. 2009), and they also use scent to find food items (Germano et al. 2014). Although chelonians are also known to discriminate shapes (Janisch 2013), we did not find any studies examining food or fruit shapes as visual stimuli, nor did we find any studies on taste discrimination.

Plants are known to employ visual and scent cues to signal ripeness in fruits to attract seed dispersers, which use these cues to assess their nutritional value (Brady 1987; Kalko et al. 1996; Schaefer et al. 2008a; Schlumpberger et al. 2006). Unripe fruits often have chemical compounds that make them unpalatable to seed dispersers (Sherburne 1972), who may learn to associate visual and scent cues with unpalatability. Therefore, we can expect that different colour and smell preferences may ultimately lead to distinct preferences for certain fruit traits. For example, many fruits are green when unripe, and yellow or red when ripe, and the ripening process is usually accompanied by the release of scents. Consequently, we can expect chelonians to have different preferences for different fruit species, be able to discern between ripe and unripe fruits, and show a preference for ripe ones, especially those that become yellow and red.

The degree to which chelonians act as valid seed dispersers rather than only as frugivores depends on the selection of fruits with viable seeds (usually ripe). Indeed, Moskovits & Bjorndal (1990) showed that the red (*C. carbonaria*)- and yellow-footed tortoises prefer fruits over other food items, and preferred fruits that

were predominantly red or yellow and were fragrant while rejecting unripe fruits. Moreover, chelonians have been observed smelling ripe and unripe fruits at close proximity before eating or apparently rejecting them. For example, this behaviour is often observed in Aldabra giant tortoises (Fig. 1c; WF and DMH, pers. obs.). Similarly, the eastern box turtle (*Terrapene carolina carolina*) seems to be able to distinguish between ripe and unripe fruits, preferring the ripe ones (Allard, 1948). However, it should be noted that Hermann's tortoises (*Testudo hermanni hermanni*) consumes unripe green fruits of *Ruscus aculeatus* (Asparagaceae) when seasonally available (del Vecchio et al. 2011), thus probably providing a limited efficiency as seed dispersers from the plant's point of view.

The only experimental study that we are aware of that simultaneously evaluated the perception of colour, olfaction and taste was by Grant (1960), studying the Texas tortoise. He proposed, based on feeding trials, that vision, olfaction, and taste, in that order, were used to by the tortoises to select food items. Thus, rather than just relying on one or the other, chelonians use sight and olfaction and taste to discriminate between possible food sources (Fitch 1965; Grant 1960; Pellitteri-Rosa et al. 2010), and when fruits and seeds become available in their habitat, they are probably effective at finding them (Moll & Jansen 1995).

Plants eaten and dispersed by chelonians

Taxonomical distribution

Chelonians consume the fruits and/or seeds of a great number of plants, including at least 588 species belonging to 368 genera in 121 families. As shown in Figure 5, these plant species are distributed across the phylogenetic tree of angiosperms. These plant species occur in many different habitats, with a variety of growth habits, and possess fruits and seeds with a myriad of traits (see Appendix 2 for the list of plant fruit and/or seed species consumed and/or dispersed by chelonians). Only 18% of all plant families had more than 10 species whose fruits and/or seeds are consumed and/or dispersed by chelonians (Table 1), with 27% of families represented by only a single plant species.

Table 1: Plant families of fruits and/or seeds most commonly eaten by chelonians.

Family	No. of spp.
Poaceae	88
Moraceae	80
Fabaceae	53
Arecaceae	52
Rubiaceae	45
Rosaceae	32
Myrtaceae	31
Asteraceae	30
Cyperaceae	24
Sapotaceae	23
Annonaceae	21
Polygonaceae	20
Malvaceae	18
Passifloraceae	17
Anacardiaceae	14
Cactaceae	14
Euphorbiaceae	13
Melastomataceae	12
Solanaceae	12
Nymphaceae	11
Urticaceae	11
Araceae	10

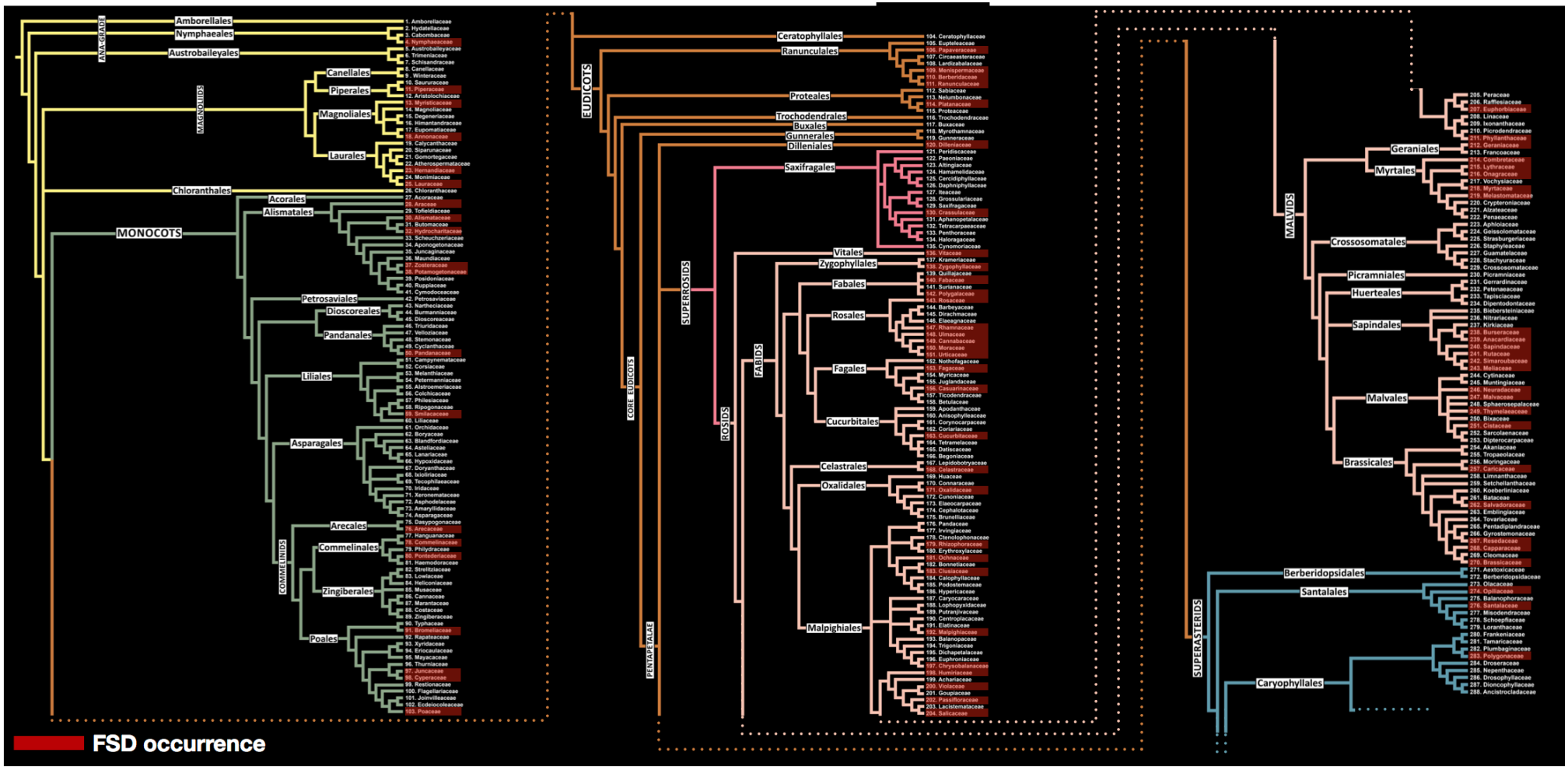

Figure 5: Taxonomical distribution of frugivory and seed dispersal by chelonian in the phylogeny of angiosperms, and representatives of the different fruits consumed by chelonians. Red shading denotes occurrence of frugivory and and/or seed dispersal in each family. Phylogeny based on The Angiosperm Phylogeny Group (2016), and figure modified from Byng et al 2018. Bars below each species of fruit scaled to 1 cm.

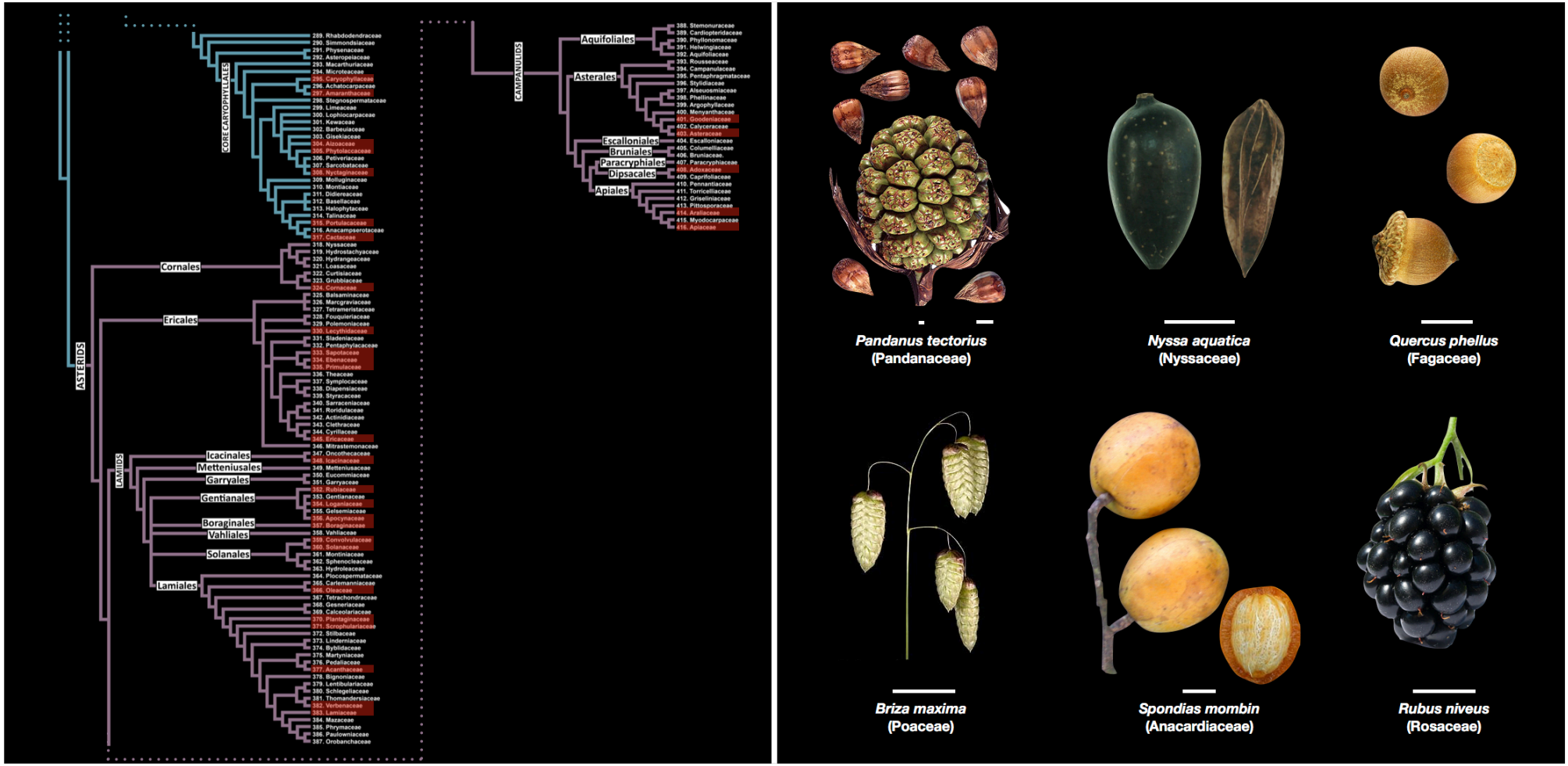

Figure 5: Cont.

Modes of dispersal

There are two modes of chelonian seed dispersal: endozoochory (dispersal of seeds through the ingestion of fruits and/or seeds), and epizoochory (dispersal of seeds on external body parts). Of these, endozoochory is by far the most common mode, forming the majority of cases reviewed in this study. It occurs in terrestrial, aquatic, and even in marine ecosystems. During the process of endozoochory, the handling behaviour, gut treatment and location of defecation all affect the ultimate quality of seed dispersal (see below). Epizoochory is a passive way of dispersal where seeds are stuck on the external parts of the animals until they are subsequently dropped, and other than movement away from the mother plant, the fruits or seeds are not affected further. Epizoochory has only been observed in two species of chelonians. The terrestrial Aldabra giant tortoises (*Aldabrachelys gigantea*), which disperse the sticky seeds of *Plumbago aphylla* (Plumbaginaceae) that adhere to their carapaces, and secondarily disperse seeds of various plant species on their carapaces after birds defecate on them (e.g., *Ficus* spp., Moraceae; WF and DMH, pers. obs.). In Australia, the aquatic eastern long-necked turtle (*Chelodina longicollis*), disperses several wetland-associated plants whose seeds lodge on its carapacial algal mats (Burgin & Renshaw 2008).

Diversity of seeds

The species diversity of seeds potentially dispersed by chelonians varies by chelonian species and/or studies. Overall, frugivorous chelonians covered in our review each potentially disperse a high diversity of seeds, with a mean of 13.0 plant species per chelonian species (± 23.6; range: 1–123; see Appendix 2 for species dispersed), and for some chelonians fruits and seeds were major parts of their diets. For example, the Gopher tortoise (*Gopherus polyphemus*) disperses more than 50 species of seeds in pine savannah in the southestern USA (Birkhead et al. 2005). For the big-headed Amazon river turtle (*Peltocephalus dumerilianus*) fruits and seeds were the most diverse components in the diet, with a total of 19 species found in the stomachs, and with Aracaceae (palm) seeds as the most common ones (Pérez-Emán & Paolillo 1997). In the northern giant musk turtle (*Staurotypus triporcatus*), the large seeds of *Diospyros digyna* (Ebenaceae) comprised 63% of the volume of their stomach

contents (Vogt & Guzmán 1988). It should be noted that although careful studies have documented many dry-seeded species dispersed, or potentially dispersed, by chelonians (e.g., Birkhead et al. 2005; Cobo & Andreu 1988; Hnatiuk 1978; Milton 1992), there is likely an underestimation in the amount and diversity of such seed species when compared to fleshy-fruited species due to the difficulty of detection and/or identification.

Plants only/mostly dispersed by chelonians

van der Pijl (1969) suggested that fruits dispersed by reptiles (saurochory) should be coloured, smelly, and borne near the ground or drop at maturity. Although strong FSD relationships have been documented between plants and some chelonians, there is a lack of evidence of coevolution that has resulted in any form of a chelonian seed dispersal syndrome (Herrera 1985). As mentioned above (see section on preferences), although they may show preferences, chelonians potentially disperse fruits with a wide variety of sizes, colours, and scents. For example, although they show preferences for certain fruits, *Chelonoidis* tortoises consume fruits with a variety of colours, including both fragrant and odourless ones (Guzmán & Stevenson 2008; Moskovits 1985).

However, certain plants may rely disproportionally on chelonians for seed dispersal. For example, while rodents and birds destroy the seeds of *Pandanus aquaticus* (Pandanaceae), gulf snapping turtles (*Elseya lavarackorum*) defecate the seeds intact (Kennett & Russell-Smith 1993). Similarly, European pond turtles (*Emys orbicularis*) disperse most of the seeds of *Nymphaea alba* (Nymphaceae) intact, while ducks, coots and fish destroy the seeds after gut passage (Calviño-Cancela et al. 2007, and references therein). Wang et al. (2011) found that red-footed tortoises (*Chelonoidis carbonaria*) may be an important seed disperser of *Syagrus flexuosa* (Arecaceae), because the seeds were often defecated undamaged but are rarely found at all in the scat of other animals. Furthermore, Moll & Jansen (1995) suggested the black wood turtle (*Rhinoclemmys funerea*) as an important seed disperser of *Ficus glabrata* (Moraceae) and *Dieffenbachia longispatha* (Araceae). This turtle is very abundant, practices “windfall” feeding in water under riparian fig trees, and emerges on riverbanks and defecates seeds while on land along shorelines in

optimal growing locations for these plants. Tortoises may also be highly important for the dispersal of large-seeded plant species on islands (Blake et al. 2012; Falcón et al. Chapter 2; Heleno et al. 2011), which has important implications at the ecosystem level (see section on chelonians as megafaunal seed dispersers).

Grasslands (composed of grasses and sedges) are an important food source in the diet of different terrestrial chelonians (e.g., eastern Hermann's tortoise, *Testudo hermanni boettgeri*; Rozylowicz & Popescu 2013). In the case of Aldabra giant tortoises on Aldabra, grasslands are the most preferred habitat (Walton et al. in review), with the high grazing pressure having led to the evolution of a specialised 'tortoise turf' plant community whose seeds they disperse (Hnatiuk 1978; Merton et al. 1976). For the green sea turtle (*Chelonia mydas*) in the Great Barrier Reef (Australia), seagrass is an important dietary component and it disperses its seeds (Tol et al. 2017). The only other known disperser of seagrass seeds in the Great Barrier Reef is the dugong (*Dugong dugon*; Tol et al. 2017), which is considered vulnerable and occurs in low numbers, and turtles may thus be more important in terms of quantity. Additionally, the diamondback terrapin is also known to be a seed disperser for eelgrass (Zosteraceae) in the Lower Chesapeake Bay (Tulipani & Lipcius 2014).

Although chelonians do not necessarily seek for grass seeds per se (but see Kimmons and Moll, 2010, turtles may eat floating grass seeds from water surface), and rather act mainly as herbivores, grasses, sedges and seagrasses in general have traits that facilitate chelonian seed dispersal. Chelonian herbivory with 'accidental' ingestion of small seeds could thus be important for the maintenance of such communities (Hnatiuk 1978; Merton et al. 1976; Tol et al. 2017); as Janzen (1984) puts it, the "foliage is the fruit". The role of chelonians as seed dispersers in grass communities is likely to be of great importance in places where they reach high densities and levels of biomass, like in island ecosystems or in some places in Africa, especially when compared to other seed dispersers (e.g., Branch 2008; Coe et al. 1979). It should be noted, however, that the six-tubercled Amazon river turtle (*Podonecmis sextuberculata*) seems to be a predator of Poaceae and Cyperaceae seeds in the Amazonas, which constituted 92% of their stomach volume contents, and whose seeds were digested (Fachín-Terán & Vogt 2014). As for any other

ingested fruits and seeds, viability, germination and/or recruitment studies are necessary to determine whether effective seed dispersal occurs.

Chelonian seed dispersal efficiency

The ultimate definition of efficient animal-mediated seed dispersal is that a dispersal event results in the successful establishment of new reproducing plant individuals. This, however, is far from always the case, as different frugivore species do not provide the same dispersal services to plants. The seed dispersal effectiveness (SDE) framework provides a way to estimate the contributions of individual dispersal agents to the overall dynamic of plant populations (Schupp 1993; Schupp et al. 2010). Essentially, it quantifies the number of seeds dispersed by a frugivore multiplied by the probability that a dispersed seed produces a new adult plant. As such, the SDE framework has two components: a quantitative and a qualitative one, which, in turn, have many variables, demographic parameters and subcomponents. The SDE framework can thus be used as a valuable organising tool to study the ecological and evolutionary implications of seed dispersal. Below we discuss chelonian FSD in the context of the SDE framework.

Quantitative component

The quantitative component of SDE can be reduced to the number of foraging visits a chelonian makes to a fruiting plant multiplied by the number of seeds dispersed for each visit (Schupp et al. 2010). The former can be affected, for example, by the local abundance of both plants and chelonians, and the chelonian's degree of frugivory, while the latter is influenced by the numbers of fruits and/or seeds handled per visit, handling behaviour, and body size (for body size, see section on chelonian functional traits).

Local biomass and density–. The most comprehensive work to date on chelonian biomass and density is that of Iverson (1982), who argued that despite the important role that reptiles play in terms of the energetics at the ecosystem level, the study of chelonian abundance and biomass was a neglected subject. He calculated biomass of chelonians based on population density estimates, and analysed those data in terms of habit, habitat, and trophic position. He found that

typical values of chelonian biomass are at least one order of magnitude higher than those of other ectotherm species. He also found indications that herbivorous chelonians, which often include fruits as part of their diet, appear to have higher biomass than omnivorous or carnivorous species. Finally, he found that annual production estimates in chelonians (with a maximum of 528 kg ha^{-1} yr^{-1}) are similar to most other vertebrate groups, except for fishes; and that the maximum biomass for individual tortoise species could be as high as 586 kg ha^{-1}. In terms of density, studies have provided estimates for several species; for example, 0.15–0.31 individuals ha^{-1}, for the highly frugivorous yellow-footed tortoise in the Amazon (Guzmán & Stevenson 2008), 0.85 tortoises ha^{-1} for leopard tortoises and 0.12 individuals ha^{-1} for angulate tortoises in South Africa (Mason et al. 2000).
In some species, chelonian biomass may be higher than that of many classes of larger mammals. For example, Branch (2008) indicated that the leopard and angulate tortoise biomass is about 13% that of all mammalian herbivores in South Africa's Eastern Cape province, where tortoises can reach high densities (Mason et al. 2000). He posited that this meant that the total biomass of tortoises there almost equalled the combined biomass of kudu, buffalo, eland, and bushbuck, only being exceeded by that of elephants! Moreover, Coe et al. (1979) estimated the biomass of Aldabra giant tortoises to range between 253.42–353.87 kg ha^{-1} on Aldabra Atoll, which is much higher than that exhibited by large mammalian herbivores on Africa. However, it should be noted that chelonian biomass is limited by different factors, such as habitat type (e.g., in mesic vs. xeric habitats; McMaster & Downs 2006), and can differ between co-occurring species (Mason et al. 2000). Nevertheless, in general, we can expect the total numbers of seeds dispersed per hectare per year to be large for chelonians (see section on quantity of seeds dispersed), especially when considering the number of large seeds dispersed (Jerozolimski et al. 2009).

Degree of frugivory–. The degree of frugivory in chelonians varies between species, and within species it can vary at the population and at the individual level. For example, in Mexican giant mud turtles (*Staurotypus triporcatus*), fruits and seeds were the most important dietary component across two sites in Los Tuxtlas (Mexico), but the occurrence of frugivory ranged from 38–100% between populations, and fruits and seeds represented values between 55–82% of the

stomach content volume examined (Vogt & Guzmán 1988). The degree of frugivory can also vary depending on the size of chelonians. For example, Sung et al. (2016) found a positive relationship between the size of big-headed turtles (*Platysternon megacephalum*) and the occurrence of fruits in their diet. Moreover, diet can vary much over short distances. Another aspect to take into consideration is the changes in diet depending on which habitat chelonians inhabit, and depending on seasons. Geoffroy's sidenecked turtle *(Phrynops (Rhinemys) geoffroanus*) may have different diets depending on whether it inhabits clean or polluted rivers (Medem 1960, cited in Fachín-Terán et al. 1995; Souza & Abe 2000), and depending on season (e.g., fruits of Myrtaceae and Sapotaceae were only found in its stomach during the season of rising water levels; Fachín-Terán et al. 1995). Likewise, the Gibba turtle (*Mesoclemys gibba* [*Phrynops gibbus*]) feeds almost exclusively on palm fruits (buriti) only during part of the year in the Rio Negro Basin in Brazil (RC Vogt, pers. comm.). Similarly, inclusion of fruits in the diet can shift seasonally in the smooth softshell turtle (*Apalone mutica*; Plummer & Farrar 1981) and the Mexican mud turtle (*Kinosternon integrum*; Macip-Rios et al. 2010). In addition, changes in diet can occur at the same location over time, as the habitat and food resources change over time (e.g., river changes from clean to polluted; Moll 1980a).

Quantity of seeds dispersed–. Propagule pressure influences the establishment of plants, and the number of seeds dispersed can thus determine the dynamics of plant recruitment. Studies on chelonians indicate that tortoises and turtles are capable of dispersing a high number and diversity of seeds. For example, in the red-footed tortoise (*Chelonoidis carbonara*), Wang et al. (2011) reported that a single scat sample contained high numbers of seeds, ranging from 22 to 765 seeds. Moreover, Lagler (1943) found 11,065 seeds of *Nymphaea alba* (Nymphaceae) in the digestive tract of ones individual of the common snapping turtle (*Chelydra serpentina*). Combining information on density estimates and information on their diet and seed dispersal ecology, Guzmán & Stevenson (2008) estimated that yellow-footed tortoises (*C. denticulata*) disperse 160.70 seeds ha^{-1} per year.

Qualitative component

The qualitative component of SDE can be reduced to the probability that a dispersed seed survives handling by chelonians in a viable condition (quality of treatment in the mouth and gut) multiplied by the probability that a viable dispersed seed will survive, germinate, and produce a new adult (quality of deposition; Schupp et al. 2010).

Mouth and gut passage treatment–. Lacking teeth, most chelonians tend to swallow fruits and seeds whole ("gulpers"), rather than chewing them as other vertebrate groups do (Moll & Jansen 1995). They use 'lingual prehension', which is the behaviour of using the tongue to touch food items to insert them into their mouths, and this is obligatory for tortoises (Bells et al. 2008; Wocheslander et al. 1999). Amphibious emydids and geoemydids use their jaws to grasp food items in terrestrial habitats, a behaviour known as 'jaw prehension' (Heiss et al. 2008; Natchev et al. 2009; Natchev et al. 2015). Moreover, and different from birds and monkeys, tortoises do not regurgitate/spit seeds. Thus, damage to seeds by the mouthparts of chelonians was minimal in the studies evaluated. For example, most of the large numbers of seeds of *Nymphaea alba* (Nymphaceae) found in the digestive tract of the common snapping turtle were mature, and very few of the coats were ruptured (Lagler 1943). However, some chelonian species can damage seeds with their mouths before gut passage. For example Caputo & Vogt (2008) reported that seeds of several plant species were never recovered whole from stomach flushing in the red side-necked turtle (*Rhinemys (Phrynops) rufipes*). Similarly, seeds of two species of plants were found crushed inside the stomachs of the giant South American river turtle (*Podocemis expansa*; Goulding 1980).

After consuming the fruits or seeds, they pass to the stomach and through the gut before being defecated. The overall effect on seeds can vary, depending on digestion efficiency and gut retention time (GRT; the time seeds take to pass through the guts until being defecated). Food intake rates may differ among food types in herbivorous chelonians, which have a flexible dietary response, with the ability of switching between cell wall fermentation and extraction of cell contents depending on the diet (Bjorndal 1989). Moreover, digestive efficiency is inversely related to

food intake in tortoises (Meienberger et al. 1993). In some instances, digestive efficiency can depend on the degree of herbivory in the species considered, and upon the types of fruits consumed (e.g., in the box turtles *Terrapene carolina* and *T. ornata*; Stone & Moll 2009). In other species, such as yellow- and red-footed tortoises (*Chelonoidis denticulata* and *C. carbonaria*, respectively), for a given diet, neither the digestibility nor the mass-specific intake varied between species, and neither did they vary by sex or body mass within each species (Bjorndal 1989).

Chelonians seem to submit digesta to a similar degree of 'gut washing' as mammalian herbivores do (Franz et al. 2011). However, although herbivorous reptiles have similar digestibilities as mammalian herbivores (Bjorndal 2012), overall, chelonians are said to be inefficient feeders because their performance at digesting cellulose is lower when compared to mammalian herbivores, and they need to eat large quantities of food to satisfy their energy demands (Branch 2008). As a result, plant items in their scat are often recognisable, and seeds often pass undamaged.

Compared to the other vertebrate groups, chelonians have relatively longer GRTs, with a mean of 7.65 days (± 5.89, for all species examined combined; Fig. 6), due to their low metabolic rates and food intake (Franz et al. 2011; Stevens & Hume 2004). Gut retention times in chelonians may be affected by a myriad of factors. For example, GRT tends to vary across seasons, especially in habitats where there are wet and dry periods (e.g., *Aldabrachelys gigantea*; Coe et al. 1979). Temperature also plays a role in regulating GRT, with increasing temperature leading to faster passage (Sadeghayobi et al. 2011). Moreover, GRT depends strongly on fruit species consumed and on overall diet composition (Bjorndal 1989; Stone & Moll 2006). For birds, secondary metabolites in fruits are known to affect GRTs (Murray et al. 1994; Wahaj et al. 1998), which is likely the case in chelonians as well. Furthermore, tortoises show variation in their intestinal morphology according to their feeding habits, and the length ratio of large to small intestines is positively related with GRT (Hailey 1997). Also, chelonians may exhibit selective food retention based on particle size (Hatt et al. 2002), with coarser food being retained for longer (Hailey 1997). Lastly, chelonians may exhibit antiperistalsis in the large intestine (i.e., contents are carried upwards; Naitoh et al. 1975), which also likely affects GRT.

Overall, mean GRT seems to increase with species size (Fig. 6), likely due to the increasing length of digestive tracts (Hatt et al. 2002). However, although mean GRT scales with body mass across different tortoise taxa, Franz et al. (2011) reported that this relationship was not significant when looking only at tortoises with body mass > 1 kg. The reported effects of chelonian size on GRT varied by species in the studies reviewed. Body size did not influence GRT in the red- and yellow-footed tortoises (Bjorndal 1989). When comparing GRT of hatchlings with that of adults of the aquatic Florida red-bellied turtle (*Pseudemys nelsoni*), Bjorndal & Bolten (1992) reported that although adults were, on average, 250 times larger, GRT was only 1.4 times longer when compared to that of hatchlings.

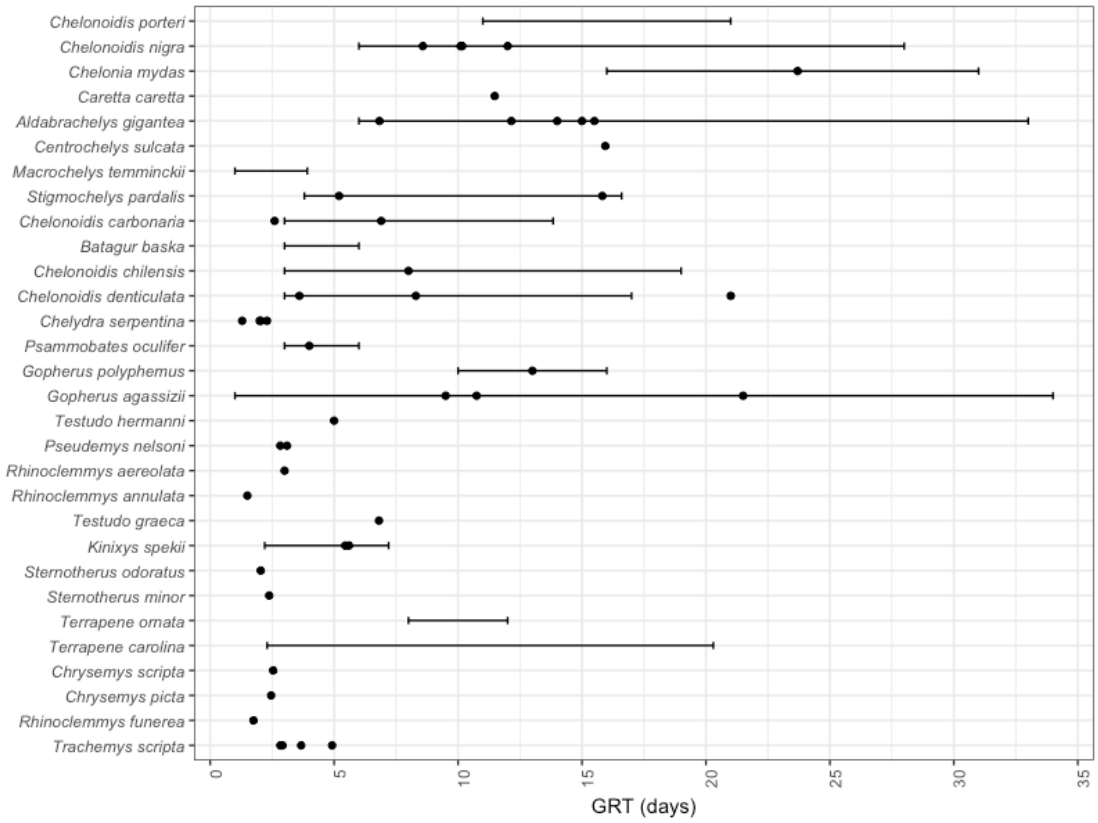

Figure 6: Gut retention times (in days) of 30 species of chelonians. Species are ordered by ascending mean body mass (bottom to top). Points represent the mean gut retention times (GRT) reported for each species by different studies, and bars represent the ranges of GRT reported (minimum and maximum). See Appendix 3 for references.

Potentially muddying the waters, studies on the effect of tortoise size on GRT in Galápagos and Aldabra giant tortoises that used different methods yielded different results. Sadeghayobi et al. (2011) found no effect of size on GRT of

Galápagos giant tortoises (carapace width range: 0.84–1.53 m) when fed artificial seeds. However, Hatt et al. (2002), using (smaller) *n*-alkanes particles as GRT markers, reported that mean GRT was shorter for smaller Galápagos giant tortoises (mass range: 7–38 kg vs. 100–210 kg in adults). Similarly, in Aldabra giant tortoises, Falcón et al. (Chapter 3) reported no effect of tortoise size (mass range: 0.6–104 kg) on GRT of artificial seeds (mean GRT 15 ± 4 days), whereas Waibel et al. (2013) reported that sub-adults (20–30 kg) had shorter mean GRT (13 ± 1 days) when compared to adult individuals (75–80 kg; 18 ± 2 days) when fed fruits of different plants. Thus, other factors such as differences in diet, hydration, food intake and temperature may be more relevant in determining chelonian GRTs within species.

Although seed size can also affect frugivore GRT (e.g., Figuerola et al. 2010; Fukui 2003), this does not seem to be the case for chelonians. Braun & Brooks (1987) found that seed size did not influence the GRT of the small, box turtle (*Terrapene carolina*) when fed fruits of different wild plants found in their habitat. Also, in larger chelonians such as the Chaco tortoise (*Chelonoidis chilensis*; Varela & Bucher 2002), the Galápagos giant tortoise (Sadeghayobi et al. 2011) and the Aldabra giant tortoise (Falcón et al. Chapter 3), seed size does not affect GRT. Overall, the GRT data suggests that within chelonian species, seeds of different sizes can be dispersed to similar distances.

Seed deposition–. After ingestion, fruits and seeds are processed in the gut and transported until they are eventually defecated. The state in which seeds are deposited by frugivores is affected by the combination of the mouth and gut treatments. In general, after handling and passage through chelonian guts, seeds are defecated without pulp, but this can be plant-species dependent as some seeds can pass with little physical change and still be covered with pulp (Hansen et al. 2008; Rick & Bowman 1961; Varela & Bucher 2002; Waibel et al. 2013). Within the same species of plants, there may be differences in terms of seed damage depending on the species of chelonian that consumes them (Kimmons & Moll 2010).

Damage to seeds tends to be minimal after defecation. For example, Rick & Bowman (1961) found that less than 1% of recovered seeds of *Solanum cheesmaniae* (Solanaceae) showed any signs of damage after gut passage. Similarly, virtually all

the seeds of *Solanum aldabrense* recovered from a single Aldabra giant tortoise scat were intact (WF, pers. obs.). Also, painted turtles (*Chrysemys picta*) pass 99% of seeds intact (Padgett et al. 2010). In addition, 90% of gut-passed seeds were intact for the red-footed tortoise (*Chelonoidis carbonaria*) in the Pantanal (Wang et al. 2011), and most seeds recovered were intact after gut passage in the yellow-footed tortoise (*C. denticulata*) in the Brazilian Amazonia (Jerozolimski et al. 2009). Even for soft seeds without endocarp, like *Syzygium mammilatum* (Myrtaceae), substantial amounts of seeds survive gut passage undamaged (Hansen et al. 2008). As a result of the minimal damage experienced by seeds after chelonian gut passage, many of them remain viable. For example, studies reported between 90–100% of viability of seeds in the faeces of red-footed tortoises (Strong & Fragoso 2006; Wang et al. 2011).

The location of seed deposition, and perhaps especially the distance from the source, are two key factors for determining what happens to seeds after defecation. This is largely affected by the frugivores' movement ecology in combination with the GRTs. Only very rarely have chelonian FSD studies specifically included movement ecology (Guzmán & Stevenson 2008; Jerozolimski et al. 2009; Moll & Jansen 1995; Strong & Fragoso 2006). We therefore here include information on the movement ecology of chelonians as it affects seed deposition, germination success and ultimately plant recruitment.

Turtles and tortoises have varied home range sizes and movement distances, and these may vary depending on species and individuals within species. There is high variation of home range size between species, with the mean home range size generally increasing with species size (Fig. 7a). Overall, chelonians have a mean home range size of 14.8 ha (± 24.2; n = 41). There is a high within-species variation in home range size (Fig. 7a). Furthermore, chelonians show overall mean daily displacements of 103.9 m day^{-1} (± 114.3; n = 22), but displacement distances do not seem to be related to chelonian size (Fig. 7b). As for home ranges, there is a high variation within species.

In contrast to many other frugivores, turtles and tortoises are mostly solitary and thus disperse seeds scattered across the landscape (Varela & Bucher 2002). Additionally, they often frequent areas expected to be of high recruitment

probability for seeds growing into plants. For example, tortoises frequent tree gaps in forested areas to bask in the sun, and such gaps are very suitable recruitment areas for many plant species. A model parameterised with red-footed tortoise cognitive data suggested that the active use of gaps by tortoises enhances the probability of seed deposition in gaps and deforested areas (Soldati 2015). Indeed, the congeneric yellow-footed tortoise (*C. denticulata*), which is a major seed disperser, often deposits seed-rich dung in open habitats and treefall gaps (Josseaume 2002, cited in Jerozolimski et al. 2009). In the wild, yellow- and red-footed tortoises favour microsites in open areas that are important for seed germination for resting, such as areas of debris piles, with fallen branches, vines or trees, where they presumably defecate more often than other sites (Moskovits & Bjorndal 1990; Strong & Fragoso 2006). Brown wood turtles (*Rhinoclemmys annulata*), are also known to frequent tree gaps (Moll & Jansen 1995). Open areas are also often used by the gopher tortoise (*Gopherus polyphemus*), which are important areas of plant recruitment in pine savannah in the southestern USA (Birkhead et al. 2005). The European pond turtles, which disperses the seeds of the aquatic waterlily (*Nymphaea alba*, Nymphaceae), effectively disperse seeds between ponds, aiding in maintaining population connectivity and meta-population dynamics of the waterlily (Calviño-Cancela et al. 2007). Moreover, even aquatic species often spend time out of the water, increasing the probability of dispersing plants to suitable habitats (rather than in the water). For example, the black river turtle (*Rhinoclemmys funerea*) in Costa Rica regularly defecates on land (Jansen 1993, cited in Moll & Jansen 1995).

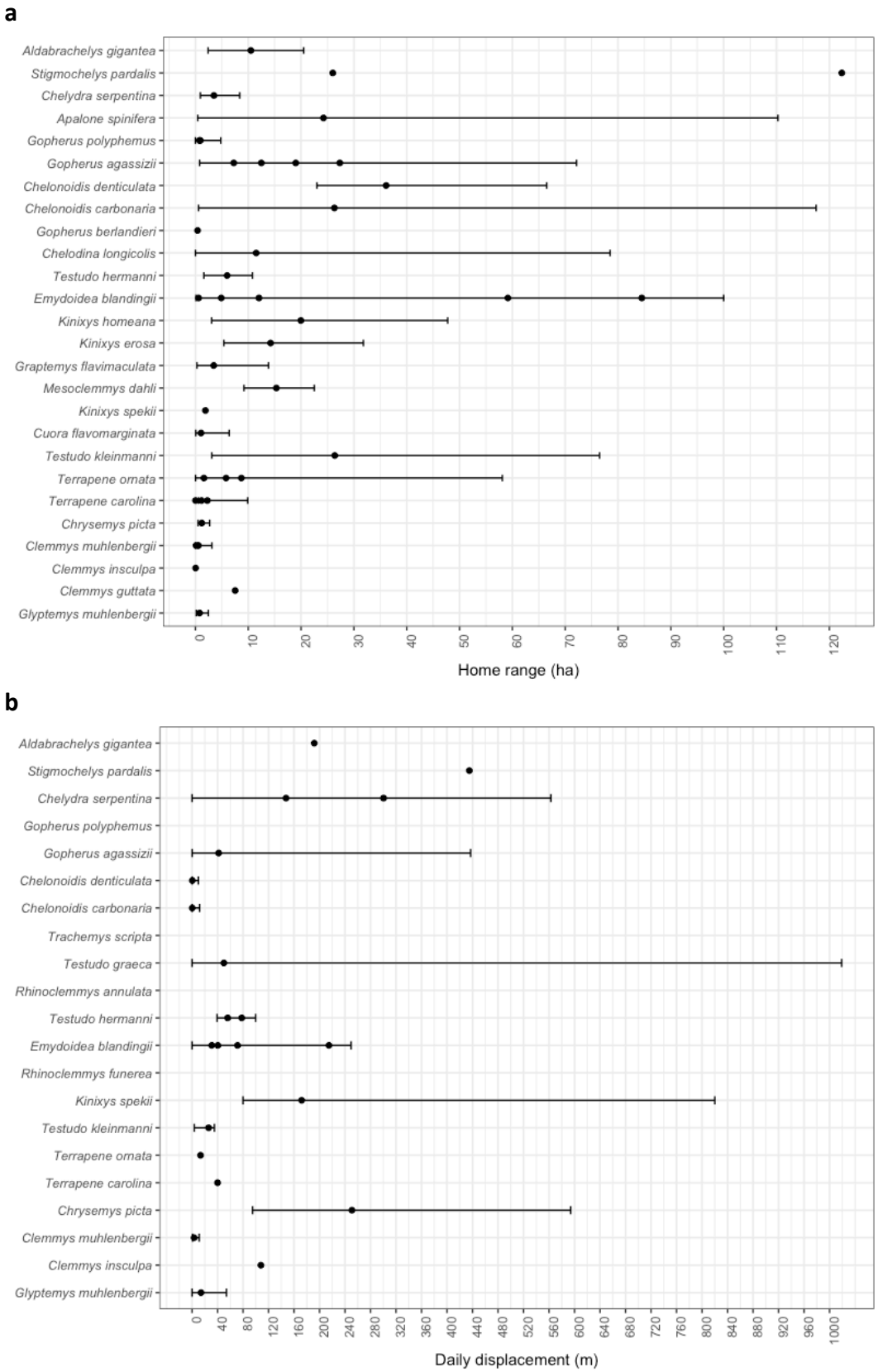

Figure 7: Home ranges (ha) and daily displacement distances (m day^{-1}) of certain species of chelonians. Points represent the mean home range and daily displacements reported for each species by different studies, and bars represent the reported ranges (minimum and maximum). See Appendix 4 (a) and 5 (b) for references.

Seed & seedling fate–. Seed deposition after zoochory has both spatial and temporal aspects, both of which affect the ultimate fate of seeds. Spatially, the Janzen–Connell model proposed that seeds that are dispersed away from maternal plants have a higher probability of survival as they can escape distance- and density-dependent seed- and seedling predation (Connel 1971; Janzen 1970). Both of these are ubiquitous interactions that result in strong establishment limitations for plants (Crawley 2000; Paine & Harms 2009; Wright 2002). Temporally, Guzmán & Stevenson (2011) proposed that escape in time via endozoochory by animals with low metabolic rates and long GRTs, such as chelonians, may aid seeds by basically allowing them to 'time travel' into the future to escape from periods with high-intensity seed predation.

After being deposited in suitable habitats, viable seeds that escape predation and pathogens may eventually germinate, and a proportion of these survive and are recruited as adult plants. One of the factors that can affect germination percentage and rates of seeds consumed by chelonians is the gut treatment. For example, gut washing by the digestive fluids of frugivores may be an important mechanism which aids in increasing seed endocarp permeability, and thus enhance germination (Traveset 1998). Germination percentage and rates can vary within plant genera and between plant species and on the frugivore species after gut passage (reviewed in Traveset 1998). Effects on seed germination after gut passage can go from positive (enhanced germination), neutral (no effect), to negative (decreased germination). In the studies reviewed here, chelonian gut passage had a mixed effect, depending on the species of chelonian and of fruits/seeds consumed (Table 2). Compared to controls (depulped seeds), 29% of the cases, gut passage had a negative effect on germination, the effect was neutral for 39% of the cases, and in 32% of the cases, seed germination was enhanced.

Table 2: Effects of chelonian gut passage on the germination percent of different plant species. Effects, compared to controls, can go from positive (+) for enhanced germination, neutral (0) to negative (–). Chelonian species are ordered alphabetically. Treatments are depicted as gut passage (GP) and controls (C). Only control treatments of depulped seeds are considered here. See Appendix 6 for references.

Chelonian species	Plant species	C (%)	GP (%)	Effect	Reference
Aldabrachelys gigantea	*Adonidia merrillii*	92.0	94.0	0	[1]
	Diospyros egrettarum	11.8	29.0	+	[2]
		12.0	46.0	+	[3]
	Adansonia fony	52.0	44.3	0	[4]
	Syzygium mamillatum	42.0	23.7	–	[5]
	Mimusops coriacea	22.3	65.4	+	[1]
	Wikstroemia indica	2.2	0.5	0	[1]
	Lantana camara	1.9	6.5	+	[1]
Chelonoidis chilensis	*Celtis pallida*	9.6	35.0	+	[6]
	Ziziphus mistol	6.4	5.0	0	[6]
Chelonoidis denticulata	*Rauvolfia micrantha*	-	-	+	[7]
	Brosimum lactescens	-	-	–	[7]
	Ficus sp. 1	-	-	+	[7]
	Ficus sp. 2	-	-	+	[7]
	Genipa americana	68.3	62.5	0	[8]
	Cecropia sciadophylla			–	[7]
Chelonoidis nigra	*Opuntia echios*	2.9	4.3	0	[9]
	Hippomane mancinella	7.5	6.0	–	[9]
	Psidium galapageium	4.0	5.5	0	[9]
	Psidium guajava	4.3	2.6	0	[9]
	Passiflora edulis	7.8	4.8	–	[9]
Chelonoidis porteri	*Solanum siparunoides*	1.0	81.0	+	[10]
Chelydra serpentina	*Morus* sp.	21.6	19.2	0	[11]
	Echinochloa crus-galli	32.7	14.4	–	[11]
	Rumex crispus	66.5	53.0	–	[11]
Emys orbicularis	*Nymphaea alba*	98.1	93.2	0	[12]
Gopherus polyphemus	*Paspalum setaceum*	17.3	10.9	–	[13]
Macrochelys temminckii	*Nyssa aquatica*	57.3	46.3	–	[14]
	Diospyros virginiana	38.0	18.4	–	[14]
	Quercus phellos	38.0	58.3	+	[14]
Platysternon megacephalum	*Machilus* sp.	3.6	37.5	+	[15]
Psammobates oculifer	*Grewia flavescens*	11.0	16.1	0	[16]
Rhinoclemmys annulata	*Jacaratia dolichaula*	60.0	50.0	0	[17]
	Faramea suerrensis	58.3	66.7	0	[17]
Rhinoclemmys funerea	*Solanum pimpinellifolium*	56.0	64.0	0	[17]
Terrapene carolina	*Arisaema triphyllum*	12.0	40.0	+	[18]
	Thrinax morrisii	19.4	11.8	0	[19]
	Podophyllum peltatum	8.5	38.7	+	[18]
		48.9	87.5	+	[20]
	Gaylussacia baccata	9.0	15.0	0	[18]
	Vaccinium vacillans	32.4	37.2	0	[18]
	Byrsonima lucida	32.3	14.4	–	[19]

Table 2: Cont.

	Morus alba	92.3	78.3	–	[18]
	Phytolacca americana	30.7	55.4	+	[18]
	Serenoa rapens	38.9	79.2	+	[19]
	Duchesnea indica	57.1	59.5	0	[18]
	Fragaria virginiana	72.0	60.5	0	[18]
	Prunus serofina	7.1	21.4	+	[18]
	Vitis aestivalis	0.0	15.0	+	[18]
	Vitis vulpina	6.7	18.5	0	[18]
	Sambucus canadensis	20.0	3.4	0	[18]
Testudo graeca	*Hypochaeris glabra*	92.0	1.0	–	[21]
	Spergula arvensis	14.0	21.0	+	[21]
	Ornithophus sativus	23.0	11.0	–	[21]
	Briza maxima	93.3	82.1	0	[21]
	Rumex bucephalophorus	55.0	15.7	–	[21]
Trachemys scripta	*Morus* sp.	21.6	19.9	0	[22]
	Echinochloa crus-galli	32.7	4.1	–	[22]
	Rumex crispus	66.5	81.1	–	[22]

In addition to depending on the species of chelonians and plants, factors such as chelonian ontogeny, seed size, within-species variation in seed dormancy, and external stimuli may affect seed germination. For example, tortoise age, which correlates with size, can affect the likelihood of seed germination after passage through the guts of Aldabra giant tortoises (*Aldabrachelys gigantea*), with smaller sub-adults increasing the probability of germination of some plant species when compared to larger adult tortoises, and this was attributed to the shorter GRTs of sub-adults (Waibel et al. 2013). Braun & Brooks (1987) found that after gut passage through the box turtle (*Terrapene carolina*), seed germination increased with increasing seed size. Plant species may also have different degrees of seed dormancy that may affect seed germination after gut passage (Rick & Bowman 1961). External stimuli, such as the availability of light can have a differential effect on aquatic seed germination, with delayed germination after gut passage in light conditions (but with equal total germination to controls), and delayed germination during the first year, with subsequent increased germination speed and percentage in the long term in dark conditions (Calviño-Cancela et al. 2007). The authors suggest that in their natural habitat, the differential effect of gut passage in combination with light stimuli is expected to affect seed germination in turbid vs. clear bodies of water. Similarly, we can expect that seeds inside the dung of terrestrial species, with no

direct light, to have a delayed germination, as dung disintegrates, and thus escape predators in time (assuming that the dung does not attract predators).

In terms of seedling growth and vigour, the few studies we found reported a positive effect of chelonian gut passage. For example, in the case of *Syzygium mammilatum* (Myrtaceae), gut passage through *A. gigantea* had negative effects on seed germination rate, but positive effects on seedling growth and health when grown 'in shitu' (i.e., grown in scat; Hansen et al. 2008). In addition, Elbers & Moll (2011) found that seeds of common persimmon (*Diospyros virginiana*, Ebenaceae) and water tupelo (*Nyssa aquatica*, Nyssaceae) had lower proportions germinations (compared to controls) after passage through the guts of alligator snapping turtles (*Macrochelys temminckii*), while the acorns of the willow oak (*Quercus phellos,* Fagaceae) had a higher proportion of germination after gut passage compared to controls. Passage of seeds of the grass *Briza maxima* (Poaceae) through the gut of the spur-thighed tortoise (*Testudo graeca*) led to seedlings growing larger and faster, although this may have been due to filtering of seed size, as only larger seeds were recorded passing through the gut (Cobo & Andreu 1988).

Secondary seed dispersal–. Secondary seed dispersal is the process by which seeds that have been initially dispersed by a frugivore via endozoochory are consumed by a second disperser, for example, through coprophagy. Some chelonian species have been observed acting as potential secondary seed dispersers. For example, giant tortoises frequently eat each other's scat on Aldabra Atoll (WF & DMH, pers. obs.), and red- and yellow-footed tortoises (*Chelonoidis carbonaria* and *C. denticulata*, respectively) have been observed eating tortoise scat in Brazil (Moskovits & Bjorndal 1990). Also, Young (2003), states that tortoises (without specifying which species) are partial to eating dung from camels, sheep, and goats, who themselves are potential seed dispersers (Kuiters & Huiskes 2010; Mancilla-Leytón et al. 2011; Root-Bernstein & Svenning 2016). Juvenile Central American river turtles (*Dermatemys mawii*) eat the scat of adults, presumably to obtain cellulolytic bacteria to aid in digestion of plant foods (Legler & Vogt 2013). Forsten's tortoise (*Indotestudo forsteni*) has been observed eating monkey scat, which contained fruit pulp (Ives et al. 2008), and thus likely also contained seeds. In addition, deer faecal

pellets were found in the scat of the box turtle (*Terrapene carolina bauri*; Platt et al. 2009). Although it is possible that they secondarily ingested some seeds from the deer scat, the authors stated that the contribution to the overall number of seeds found in the turtle's dung is likely to be minimal. Also, North American box turtles (*T. carolina* and *T. ornata*) regularly eat cow dung which often contains seeds (DM, pers. obs.)

Seeds in tortoise scat can also be potentially secondarily dispersed by non-chelonian species. For example, turtle doves (*Streptopelia picturata*) have been observed eating the contents of giant tortoise scat on Aldabra Atoll (WF, pers. obs). Moreover, dung beetles, which feed on scat and usually bury it, have been recorded amassing and dispersing scat of red- and yellow-footed tortoises in Brazil (Strong & Fragoso 2006). In addition, land crabs (*Cardisoma carnifex*) and coconut crabs (*Birgus lastro*) have been observed eating giant tortoise scat containing grass and *Ficus* sp. seeds on Aldabra Atoll (WF, pers. obs.). We are unaware of any studies addressing the effects of secondary seed dispersal by chelonians, or other species consuming chelonian scat, on plant germination and/or recruitment and it thus remains to be seen whether effective secondary seed dispersal occurs in, or is promoted by, chelonians.

Chelonian FSD in a community context

The interactions between plants and frugivores do not occur in a vacuum, but are embedded in the ecological network of seed dispersal interactions between all plant species and all frugivores in the community (Bascompte & Jordano 2007). Therefore, if we truly want to know the role of chelonians as seed dispersers, we must look at their role in a community context. Studies on the role of chelonians as frugivores and seed dispersers at the community level are scarce (we found only four studies, described below) yet they provide valuable insights about their role in relation to other frugivores.

Donatti et al. (2011) studied seed dispersal interactions at the community level in the Brazilian Pantanal using bipartite interaction network analysis. For mutualistic plant–animal interactions, a bipartite network consists of nodes (vertices) and links (edges), which are represented by trophic levels (i.e., frugivores

and plants in this case) and the interactions between them (interactions within trophic levels are not possible). The Pantanal seed dispersal network was hyper-diverse, with 46 species of frugivores interacting with 46 species of plants. In the network, the red-footed tortoise (*Chelonoidis carbonaria*), was the sixth most important frugivore in terms of the number of interactions (Fig. 8a). Given the diversity and the complexity of the network, based on the number of interactions in comparison to other frugivores and the fact that they are capable of dispersing large-seeded plants, red-footed tortoises are probably one of the most important dispersers in the Pantanal community.

Falcón et al. (Chapter 2) studied seed dispersal interactions in the smaller plant–frugivore community of Aldabra Atoll (with ten frugivores and 37 plant species), home to Aldabra giant tortoises (*Aldabrachelys gigantea*). The network was highly generalised, and tortoises were the second most important seed dispersers in terms of the number of interactions. In total, *A. gigantea* dispersed the seeds of at least 20 fleshy-fruited plant species (grasses and sedges were not included; Fig. 8b), including large-seeded ones such as *Cordia subcordata* (Boraginaceae) and *Guettarda speciosa* (Rubiaceae). Moreover, they found that the network was most vulnerable to the loss of three particular frugivores, one of them being the giant tortoises. This study highlighted the importance of tortoises as megafaunal seed dispersers and suggests that the many recently extinct giant tortoises in the Indian Ocean (see Hansen et al. 2010) had a similarly pivotal role in their communities before being exterminated.

In Galápagos, Heleno et al. (2013) used network analysis to investigate the impact of alien plants on the seed dispersal networks in two islands, one of which harboured giant tortoises (*Chelonoidis nigra*). They looked at the seed dispersal of both native and introduced plants by the different island frugivores. Giant tortoises here were the third most important seed disperser in terms of the number of interactions (Fig. 8c), and were especially important for fleshy-fruited plants. They also performed an analysis of the quantitative seed dispersal network, and stated that tortoises played an important role as seed dispersers based on the strength of interactions, and that the extirpation of tortoises on other islands in the Galápagos

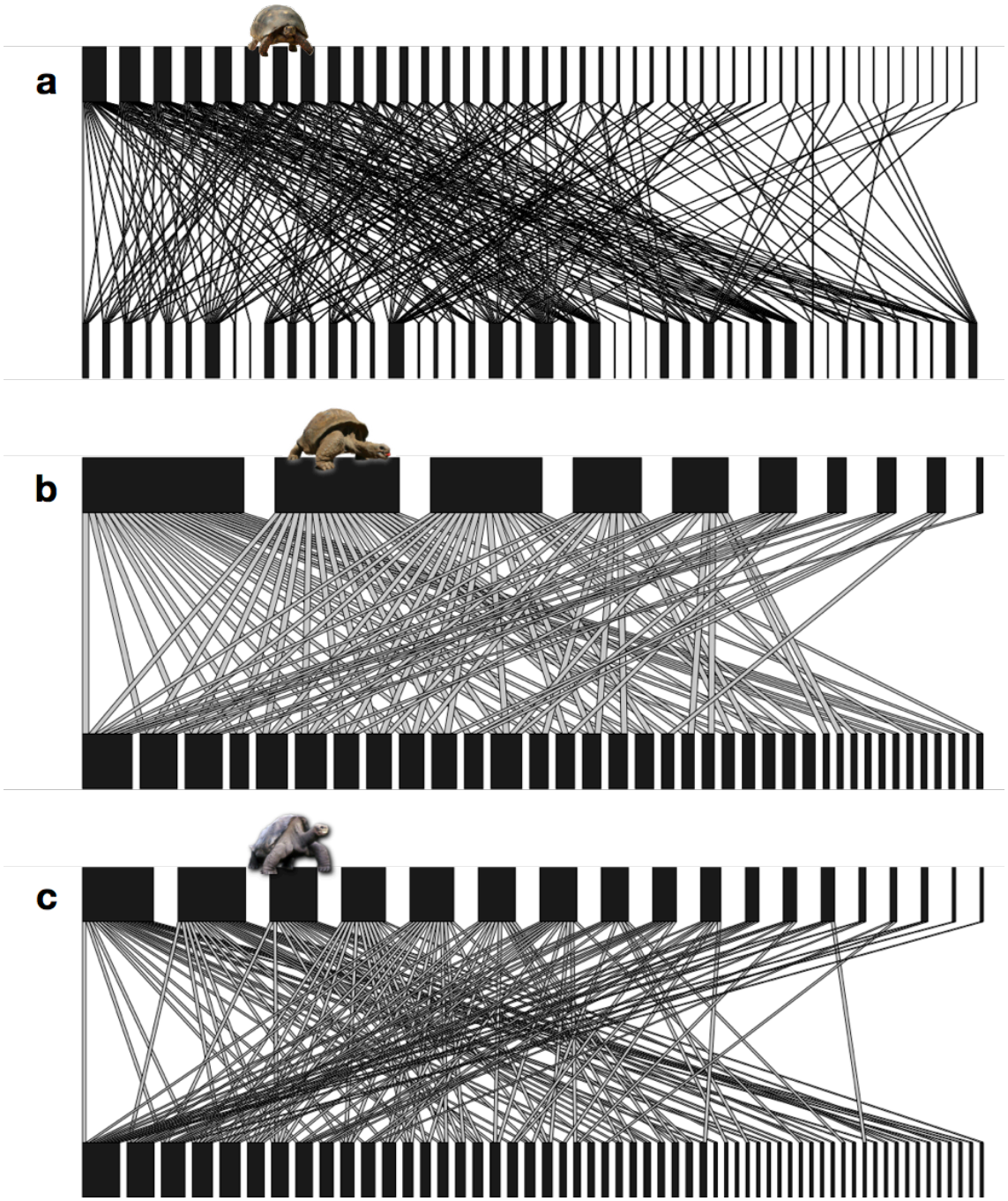

Figure 8: The role of chelonians as frugivores and seed dispersers in a community context, based on the seed dispersal networks of Pantanal (a; *Chelonoidis carbonaria*), Aldabra Atoll (b; *Aldabrachelys gigantea*), and Galápagos (c; *Chelonoidis nigra*). Networks are qualitative (i.e., the strength of the interactions are not considered) and the size of the boxes represent the number of interactions for each frugivore (top; organised from largest to smallest) and each plant (bottom) present in the community. Networks drawn from data available in Donatti et al. (2011; a), Falcón et al. (Chapter 2; b), and Heleno et al. (2013; c).

must have resulted in a negative impact on seed dispersal function at the community level.

Also in the Galápagos, Nogales et al. (2017) took a step further and studied the direct contributions delivered by different groups of frugivores, including giant tortoises, lizards, and three groups of birds, to the number of seeds dispersed, and the effect on germination. Frequency of occurrence of seeds was the highest in the scats of giant tortoises and medium-sized passerine birds, but the number of seed deposited per unit area was lowest for tortoises and lizards. In terms of seed emergence after gut passage, only a small proportion of seeds from all scat samples germinated (19%) within the study period, but those that originated from tortoise scat showed the highest emergence frequency compared to seeds dispersed by all the other disperser guilds. Based on the large frequency of occurrence and number of seeds found in the scat, as well as seed germination after gut passage, they concluded that Galápagos giant tortoises play a key role as seed dispersers in the Galápagos Islands.

Chelonians as megafaunal seed dispersers

On many islands worldwide, large and giant tortoises were present until recently, and were often the largest vertebrates in their respective faunas (Hansen et al. 2010). Giant tortoises on islands function as megafauna, capable of dispersing even very large seeds (Hansen & Galetti 2009). Surprisingly, there is evidence that medium-sized tortoises in continental ecosystems can disperse unexpectedly large seeds. In Amazonia, Jerozolimski et al. (2009) found that yellow-footed tortoises (*Chelonoidis denticulata*), a tortoise with a mean length of 40 cm, dispersed seeds of the palm *Attalea maripa* (Arecaceae) of up to 40 x 17 mm, and Mitchell & Daly (1998) described how *C. denticulata* tortoises easily swallowed the 50–60 mm large fruits of *Spondias testudinis* (Anacardiaceae), thus presumably capable of dispersing the ca. 40 x 30 mm large seeds. The two Brazilian *Chelonoidis* species may thus act as some of the last surviving heirs to several of the many large-seeded fruits left orphaned by late Pleistocene megafauna extinctions (Guimarães et al. 2008), and *Spondias mombin* is thus perhaps not yet entirely “culturally deprived in [mammalian] megafauna-free forest" (*sensu* Janzen 1985).

Chelonian FSD and conservation/restoration

Chelonians are the most endangered of the major groups of vertebrates, exceeding birds, mammals, fishes and amphibians (van Dijk et al. 2014). Factors that affect the conservation of chelonians include habitat destruction, exploitation, and climate change. On a more positive note, chelonians have shown themselves to be key players in habitat restoration projects.

Chelonian conservation

Roll et al. (2017) found that the distributional overlap of the range of chelonians with protected areas is only ca. 10%, which puts them at great risk, especially if they are habitat specialists. For example, the Northern Australian snapping turtle (*Elseya dentata*) resides in riverine habitats, and their diet consist mainly of fruits of riparian rainforest trees, so they are particularly vulnerable to changes in land management that may have negative effects on riparian forest habitats (Kennett & Tory 1996). Thus, habitat modification and destruction not only affect chelonian populations, but can also affect the availability of fruit resources, which can lead to the loss of seed dispersal mutualisms.

Exploitation is another factor threatening the conservation of chelonian species, and the main causes are consumption as food resources, traditional medicine, and the pet trade. Known frugivorous chelonians are not exempt from suffering from exploitation, and for example, species of the turtle genera *Trachemys* and *Pseudemys* are the most exported turtles in the USA, with individuals being taken directly from the wild, or taken from the wild and subsequently bred in captivity (Mali et al. 2014; Moll & Moll 2004). Similarly, species such as the radiated tortoise (*Astrochelys radiata*; Leuteritz 2003) and the spur-thighed tortoise (*Testudo graeca*; Walker & Rafeliarisoa 2012), are prone to exploitation from their native habitat. Exploitation of chelonian populations may have important implications for seed dispersal as the reduction of frugivore populations can result in the functional extinction of seed dispersal mutualisms, even before the species of frugivore itself goes extinct (e.g., McConkey & Drake 2006).

In addition, changes in temperature and precipitation due to anthropogenically-induced climate change are poised to affect many ectothermic species, including chelonians, harder than endothermic ones (Clusella-Trullas et al. 2011; Deutsch et al. 2008; Ihlow et al. 2012; Walther et al. 2002). For example, turtle and tortoise species may respond strongly to precipitation, and their activity and movements decrease with increasingly dry periods (Baxter 2015; Falcón et al. 2018; Chapter 4; Luiselli 2005). In addition, increasing droughts can affect the habitats of chelonians (Haverkamp et al. 2017), and potentially reduce shade availability, which is an important resource for thermoregulation (Merton et al. 1976; Moulherat et al. 2014). Moreover, increasing temperatures have been shown to decrease the activity of chelonians, and they may be particularly vulnerable to increases in air temperature in terms of thermoregulation (Falcón et al. 2018; Chapter 4; Lambert 1981; McMaster & Downs 2013). Thus, the magnitude and outcome of chelonian FSD is very likely to be negatively affected by climate change.

Rewilding and restoration

Overall, because frugivorous chelonians in general are efficient seed dispersers they are ideal candidates for rewilding and restoration efforts that have the resurrection of extinct seed dispersal interactions as a major focus. This is especially the case in island ecosystems, where many of the large-bodied frugivores have gone extinct (Heinen et al. 2017), and where giant tortoises are in general considered to be ecosystem engineers (Hansen et al. 2010). The best-studied example of this is the introduction of Aldabra giant tortoises to islands in the Mascarenes to restore the function left behind by the extinction of the endemic *Cylindrapsis* giant tortoises (Griffiths et al. 2010; Hansen et al. 2010). Here, they effectively disperse the seeds of several endemic and endangered plant species (Griffiths et al. 2010; Hansen et al. 2008), including the large-seeded *Diospyros egrettarum* (Ebenaceae; Griffiths et al. 2011). Moreover, these tortoises have also been shown to have potential as seed dispersers of the huge fruits of Baobab trees (*Adansonia rubrostipa*, Malvaceae) in Madagascar, where giant tortoises also used to occur (Andriantsaralaza et al. 2013),

and may soon find themselves being deployed as ecological restoration agents in Madagascar, too (Pedrono et al. 2017).

The perhaps most 'extreme' functional substitution can be found in Hawai'i, where recently extinct herbivorous and frugivorous giant flightless ducks and geese have been replaced by the large African spurred tortoise (*Centrochelys sulcata*) in the Makauwahi Cave Reserve on the island of Kauai (Burney et al. 2012). Although neither terrestrial nor fresh water chelonians ever reached Hawai'i by natural means, based on their ecology, the authors posited that the spurred tortoises could act as ecological substitutes for the extinct endemic frugivore-herbivores.

Rewilding with tortoises does not have to be necessarily limited to islands, and according to Sobral-Souza et al. (2017), the continental northern Atlantic Forest of Brazil, which is heavily defaunated and fragmented, and whose fragments are too small to reintroduce large mammalian frugivores, is another potential tortoise rewilding region. Based on studies highlighting the role of yellow- and red-footed tortoises as seed dispersers (*Chelonoidis denticulata* and *C. carbonaria*, respectively), especially for large-seeded plants, and on the success of rewilding efforts with Aldabra giant tortoises, the authors argued that introducing these *Chelonoidis* spp. in fragments of the northern Atlantic Forest would be a way to mitigate the negative cascading effects of defaunation. To support their argument, they employed niche modelling based on known occurrence of tortoises, and assessed food availability and conservation co-benefits, and found that fragments in the northern Atlantic Forest are suitable for these tortoises.

Conclusions

(1) Chelonian FSD is geographically and taxonomically widespread. In contrast to other major classes of frugivorous reptiles, chelonian FSD is not mainly restricted to islands. However, and different to patterns of chelonian species richness, most FSD studies in turtles and tortoises come from the Southeastern USA and northern South America. Studies on chelonian FSD in Southeast Asia, where chelonian species richness peaks, are notably scarce.

(2) Chelonian FSD occurs widely across the angiosperm phylogeny, with at least one family represented in all of the major grades and clades. There is, however,

an asymmetry of interactions, in which few plant families amass most of the unique pairwise interactions with chelonians.

(3) Based on the studies reviewed here, we expect frugivorous chelonians to be, in most cases, efficient seed dispersers. Not only they can consume large quantities and a high diversity of fruit and/or seed species, but the damage by the mouth parts or after passage is minimal, resulting in many viable seeds. Moreover, compared to controls, passage of seeds through chelonian guts seldom causes negative impacts on seed germination, but indeed often result in neutral to positive effects, and can lead to high seedling vigour.

(4) Seed dispersal interactions do not occur in a vacuum, and the few studies that have investigated the role of chelonians from a community perspective have highlighted their importance in terms of not only the number and strength of interactions, but also the importance of their role as central species amongst frugivores in seed dispersal networks.

(5) Large and giant tortoises (Testudinidae) were present on many islands worldwide until recently, and were often amongst the largest vertebrates. It is in islands, especially, where they are/were prime dispersers of large-seeded plants. Nonetheless, the capacity of large testudinid species in continental ecosystems as megafaunal seed dispersers has also been demonstrated. Therefore, chelonians can act as megafaunal seed dispersers in many ecosystems globally.

(6) Finally, on the one hand, chelonians are amongst the most threatened taxa in the world. Not only they suffer from habitat loss and lack of protection, but they are also heavily exploited, and face an uncertain future due to pressures imposed by climate change. On the other hand, chelonians have a great potential to aid in the conservation of plant–frugivore mutualisms—which have vital implications for ecosystem functioning—and to be used as analogue species to restore lost interactions and functions.

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2

THE ALDABRA SEED DISPERSAL NETWORK: AN INTACT PLANT–FRUGIVORE ASSEMBLAGE ON AN OCEANIC ISLAND

CHAPTER 2

The Aldabra seed dispersal network: An intact plant–frugivore assemblage on an oceanic island

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Abstract

Recent studies on mutualistic networks have highlighted the importance of plant–animal interactions in shaping biodiversity, and have prompted calls to focus on the conservation of the structure of interactions. Animal-mediated seed dispersal is an important ecological function in many ecosystems, and the complexity of these interactions at the community level is a good example of species interaction networks. Here, we evaluate the virtually intact seed dispersal network (SDN) of Aldabra Atoll in the Western Indian Ocean. Aldabra is one of the few islands with an almost intact vertebrate fauna, comprising lizards, birds, fruit bats, and giant tortoises. To construct a robust SDN of Aldabra, we employed three field methodologies to sample plant–frugivore interactions: observations, camera traps, and faecal analysis. In addition, we surveyed published and grey literature on plant–frugivore interactions on Aldabra, and combined the data to that of our empirically derived network to construct a full network. We investigated structural parameters and identified potential drivers and hub species of the SDNs. We recorded a total of 367 seed dispersal events in the field. There was a 40% overlap between the empirically- and the literature-derived SDNs, with 38 interactions only recorded in the field, and 22 interactions only recovered from the literature. Notably, the literature increased the number of unique pairwise interactions from 78 to 100, highlighting the utility of including this source when constructing SDNs. In the full network, these 100 interactions occurred amongst 10 frugivores and 37 plant species. The full Aldabra SDN had a connectance of 0.27, was nested (NODF = 57.25, $z = 8.61$, $p < 0.001$), and exhibited no modularity. Blue pigeons, Aldabra giant tortoises and bulbuls were the most central species in the SDN, and thus potential drivers of its structure. Closely related species of these frugivores have gone extinct on other islands in the Western Indian Ocean, and we discuss conservation implications for the functional resurrection of biotic interactions. Overall, the Aldabra SDN has a great potential as a functional baseline to inform restoration and conservation efforts at the community level on highly degraded islands in the Western Indian Ocean.

Keywords: *seed dispersal, networks, plant–animal interactions, conservation, Aldabra Atoll*

Resumen

Estudios recientes sobre redes mutualistas han resaltado la importancia que tienen las interacciones planta–animal en moldear la biodiversidad, y esto ha resultado en pedidos para enfocarse en la conservación de la estructura de dichas interacciones. La dispersión de semillas mediada por animales es una función ecológica importante en muchos ecosistemas, y la complejidad de estas interacciones al nivel de la comunidad es un buen ejemplo de las redes de interacciones de especies. En este estudio, evaluamos red de dispersión de semillas (RDS) de Aldabra. Aldabra es una de las pocas islas con una fauna de vertebrados casi intacta, que incluye lagartijas, aves, murciélagos fruteros y tortugas gigantes. Para construir una RDS de Aldabra robusta, empleamos tres metodologías para el muestreo de interacciones plantas–frugívoros: observaciones, trampas de cámaras y análisis fecal. También revisamos literatura 'gris' y publicada sobre interacciones plantas–frugívoros en Aldabra, y combinamos estos datos con aquellos derivados empíricamente para construir una RDS completa. Investigamos los parámetros estructurales e identificamos a las especies que potencialmente actúan como impulsores y focos de la estructura de la RDS. Detectamos un total de 367 eventos de dispersión de semillas en el campo. Hubo un entrelazamiento de 40% entre la RDS empíricamente derivada y la derivada de la literatura, con 38 interacciones únicas solamente detectadas en el campo y 22 interacciones únicas solamente recobradas de la literatura. Notablemente, las interacciones de la literatura incrementaron el número de interacciones únicas de 78 a 100, resaltando la utilidad de incluir dicha fuente al construir RDS. En la red completa, éstas 100 interacciones ocurrieron entre 10 frugívoros y 37 plantas. La RDS de Aldabra completa tuvo una conectancia de 0.27, fue anidada (NODF = 57.25, $z = 8.61$, $p < 0.001$), y no exhibió modularidad. Las palomas de Comoro, las tortugas gigantes, y los bulbuls fueron las especies más centrales en la RDS de Aldabra, y, por consiguiente, impulsores potenciales de su estructura. Especies relacionadas a éstos frugívoros se han extinguido en otras islas al oeste del Océano Índico, por lo que discutimos las implicaciones de la resurrección de interacciones bióticas para la conservación. Visto en conjunto, la RDS de Aldabra tiene un gran potencial para servir como una base funcional para informar esfuerzos de restauración y

conservación a nivel de la comunidad en islas del oeste del Océano Índico, las cuales están altamente deterioradas.

Introduction

Islands and fruigvores

Oceanic islands possess fewer species compared to continental ecosystems, but they harbour a disproportionately large share of the world's biodiversity (Kier et al. 2009). Most island ecosystems have suffered from negative anthropogenic impacts, especially habitat loss, overharvesting, and invasive alien species that have led to multiple species extinctions (e.g., Brooks et al. 2002; Fordham & Brook 2008). These extinctions have resulted in the disruption of species interactions, which further threatens the remaining native biodiversity (Paulay 1994; Brooks et al. 2002; Blackburn 2004; Kaiser-Bunbury et al. 2010). One such disrupted ecological process is animal-mediated seed dispersal (zoochory; hereafter 'seed dispersal') through the extinction of frugivores. Seed dispersal is the process in which seeds are dispersed away from the parent plants by frugivores –usually by offering the latter nutritional benefits. It is considered an vital ecosystem function that structures plant regeneration and biodiversity, especially in the tropics, and has profound ecological and evolutionary implications in ecosystems (Howe & Smallwood 1982; Rezende et al. 2007; Stoner & Henry 2008).

The role of different groups of vertebrates—e.g., primates, rodents, pigeons, passerines, fruit bats and lizards—in seed dispersal on islands has been intensely studied for decades (summarised in, e.g., Estrada & Fleming 1986; Dew & Wright 1998; Levey et al. 2002). In many island ecosystems, studies have highlighted the importance of birds and mammals (bats) as important seed dispersers (e.g., Howe & Smallwood, 1982). For example, birds and bats in particular have been shown to be important for introducing zoochorous plant species to the isolated island of Krakatau after it was sterilised by a volcanic eruption in 1883 (Whittaker & Jones 1994). In New Zealand, 70% of woody plants depend on animals for seed dispersal, and the majority of these plants have evolved for seed dispersal by birds; in turn, roughly 70% of New Zealand bird species consume fruits (Clout & Hay 1989). Moreover, fruit bats have been considered keystone seed dispersers in the Pacific islands and Mauritius (Cox et al. 1991; Florens et al. 2017), and have a predominant role in the dispersal of early successional woody vegetation (Muscarella & Fleming 2007). Additionally, the key role of lizards and tortoises as important seed dispersers in

island ecosystems has been highlighted (reviewed in Olesen & Valido 2003; Falcón et al. Chapter 1), and some disperse the seeds of endangered plants (e.g., Traveset & Riera 2005; Griffiths et al. 2011). Only recently researchers began studying seed dispersal at the community level on islands, of which many have been substantially compromised by the reduction of diversity of their frugivore assemblages.

Most islands have experienced frugivore extinctions during the Holocene, with an average of 24% decrease in the frugivore communities (Heinen et al. 2017). Moreover, frugivore extinctions are often biased towards larger animal species, especially on islands (Guimarães et al. 2008; Hansen & Galetti 2009; Heinen et al. 2017). Notably, frugivores whose densities decline significantly cease to function as effective seed dispersers before they become extinct (McConkey & Drake 2006). These extinctions and functional extinctions of frugivores may lead to a reduction in the diversity of –or the collapse of– seed dispersal mutualisms in the communities, which can result in rapid evolutionary change in key plant/fruit traits (Galetti et al. 2013), reduced plant population connectivity (Pérez Méndez et al. 2017), or bottlenecks and plant extinctions (Bond 1994). However, secondary extinctions can be circumvented when other animals in the community expand their diet breath, switch to resources that become available due to disappearing mutualists, or when a new species is introduced, thus filling the gaps of missing interactions (Kawakami et al. 2009; Kaiser-Bunbury et al. 2010). The different functional and dynamic roles of individual frugivores, thus, highlight the importance of considering seed dispersal at the community level.

Interaction networks

A detailed understanding of seed dispersal mutualisms at the community level is not easy to achieve because the interactions between plants and frugivores do not occur in a vacuum, but are embedded in the ecological network of seed dispersal interactions (SDN) between all plant species and all frugivores in the community (Bascompte & Jordano 2007). Studying seed dispersal and assessing the role of seed dispersers in structuring plant communities is progressively being achieved by using graph theory, specifically a bipartite network approach, which allows the consideration of all the players that take part in the interactions matrix. For

mutualistic plant–animal interactions, the bipartite network consists of nodes (vertices) and links (edges), which are represented by trophic levels (e.g., frugivores and plants) and the interactions between them (interactions within trophic levels are not possible). The application of graph theory to mutualistic interactions, usually encompassing pollination as well as seed dispersal, has advanced rapidly in recent years, allowing researchers to address broad-scale questions on the community-level structure of mutualistic interactions (Bascompte & Jordano 2007; Olesen et al. 2007; Vázquez et al. 2009).

Mutualistic networks, including pollination and seed dispersal networks, have certain structural attributes in common. For example, interaction asymmetry where species with few links interact predominately with species that have many links, and nestedness where specialist species interact with a sub-set of the species that a generalist interacts with (Bascompte & Jordano 2007). Seed dispersal networks tend to show an imbalance in the relative number of frugivores and plants in the network, with a general plant–frugivore ratio of 2:1 (Guimarães et al. 2007). Moreover, some networks exhibit modularity (e.g., Donatti et al. 2011), which is the presence of groups (or compartments) of species that interact more frequently with each other within the group, and having relatively few links to other groups (Olesen et al. 2007). In addition, modularity analyses on avian seed dispersal networks have shown the dominating impacts of ecological factors, such as climatic variables, on their structure, and also underscore the relevance of evolutionary history in shaping the role of species in ecological communities (Schleuning et al. 2014). In plant–pollinator networks, modularity has been associated with network size, with larger networks being more likely to show modularity than smaller ones. Furthermore, the topology of pollination networks has been associated with their functioning, where changes in the composition of pollinator assemblages has profound implications on the plant population performance and local persistence (Gómez et al. 2011).

In addition to enabling scientists to study seed dispersal at the community-level, the application of network theory, together with simulations and statistical analyses, has also allowed ecologists to examine interaction robustness in relation to different perturbations (e.g., extinctions; Rezende et al. 2007; Bascompte & Stouffer 2009; Kaiser-Bunbury et al. 2010; Menke et al. 2012). Another aspect of network

theory applied to mutualistic interactions is the possibility of identifying important species and interactions that determine the structure of the network (e.g., acting as connector or hub species) through the use of centrality and vulnerability measures (Sazima et al. 2010; Martín González et al. 2010; Mello et al. 2015; García-Algarra et al. 2017). Overall, the analytical methods of bipartite networks provide ecologists with a diverse toolkit to dissect the layers of the structure of seed dispersal interactions at the community level.

Aldabra Atoll as an SDN model system

Different from other islands in the western Indian Ocean, and indeed from most islands around the world, Aldabra Atoll, Seychelles (Fig. 1), has a virtually intact native assemblage of frugivores and plants. Despite the relatively young age of Aldabra (max of 120–130,000 yr; Braithwaite et al. 1973), the frugivore fauna also contains most of the components that once characterised frugivore assemblages on many older and larger islands in the Indian Ocean prior to human arrival. Thus, Aldabra is one of the very few ecosystems in the world, including continental ones, which still has its full size-range of potential frugivores, from a megafaunal giant tortoise to small lizards and passerine birds. Similarly, Aldabra's flora of animal-dispersed fleshy-fruited plants is species-poor but diverse, displaying a wide range of fruit traits, such as size, colour, amount of pulp, and phenology. Given the level of defaunation in many ecosystems worldwide, understanding the structure and processes of an almost intact plant-seed disperser community provides critical insights for species conservation, including re-introductions and translocations, ecosystem restoration and re-wilding in island and mainland ecosystems alike.

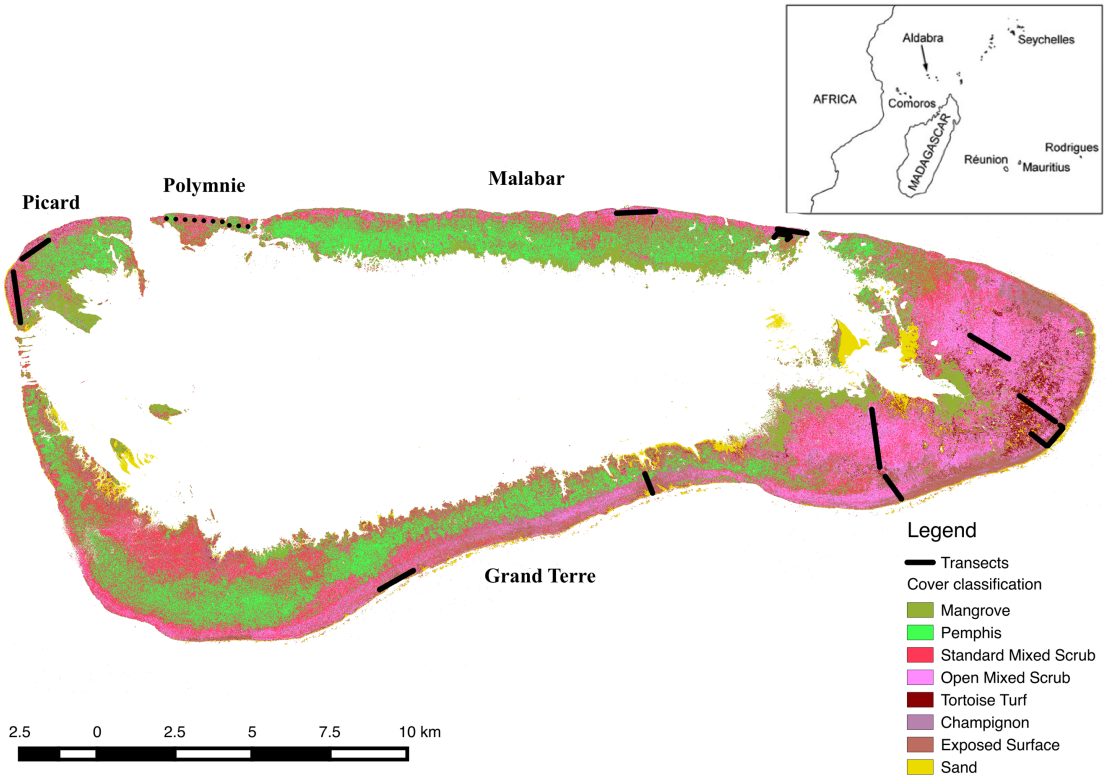

Figure 1: Map of Aldabra Atoll, Seychelles, indicating the major cover classifications and monitoring transects (black lines). Map modified from Walton et al. in review.

Study aims

Here, we construct the seed dispersal network (SDN) of Aldabra Atoll to examine key structural features of an intact island plant–frugivore community. The network is based on extensive frugivory and seed dispersal (FSD) field observations and a compilation of interaction records from the literature. We first construct and describe the topological, structural, and ecological properties of the network. We then zoom in on the plant and frugivore level, respectively, to determine their robustness to perturbations, and to the species level to determine the relative importance of individual species of plants and frugivores in terms of centrality and vulnerability in the network.

Based on our current understanding of the structure and proposed mechanisms of assembly of mutualistic networks (Olesen et al. 2007; Vázquez et al. 2009; Bascompte & Stouffer 2009), and the comparably small size of the potential

network, we expect that the Aldabra seed dispersal network will be nested and only consist of one module (i.e., no modularity). Moreover, because Aldabra still has a complete range of native frugivore and plant species, we expect a high level of redundancy and consequently a system robust to disturbances.

Methods

Study system

Aldabra Atoll, in the south western Indian Ocean (SWIO), has a land area of 155 km^2, and consists of four major islands: Grande Terre (116 km^2), Malabar (27 km^2), Picard (9 km^2), and Polymnie (5 km^2), encircling a large lagoon, and is managed by the Seychelles Islands Foundation (SIF; Fig. 1). Aldabra is a tropical atoll, with year-round high temperatures (mean range: 24–28˚C), and 975 mm of mean annual rainfall (Shekeine et al. 2015). The atoll has a pronounced seasonality in precipitation, with a wet season from November-April (mean monthly precipitation of 118.4 mm ±23.1), and a dry season from May-October (mean monthly precipitation of 30.6 ±7.7). A large part of the atoll is covered in either thick coastal scrub, or a mixture of trees, herbs and grasses, and the majority of fleshy-fruited plants occur within the mixed- and standard scrub habitats (Gibson & Phillipson 1983; Walton 2015; Fig. 1). The dominant terrestrial habitat types on the atoll are standard mixed scrub (43.3 km^2), followed by pemphis scrub (35.8 km^2), open mixed scrub (25.4 km^2), and grassland (4.5 km^2; Walton et al. in review). Aldabra supports an almost intact native fauna and flora with very few invasive species (e.g., rats, cats) on some islands. There has been only one known avian species extinction, the Aldabra brush warbler. Reflecting its uniqueness, Aldabra was declared a UNESCO World Heritage Site in 1982.

The potential vertebrate frugivore guild is small, but highly diverse, comprising a total of 15 species of birds, mammals, reptiles, and terrestrial crabs. Their dietary specialisation varies from obligate, partial, to opportunistic frugivory (*sensu* Kissling et al. 2009). On the plant side, there are 51 fleshy-fruited species on the atoll (approx. 40% of Aldabra's flora, excluding grasses and sedges) belonging to

36 families (*sensu* Fosberg & Renvoize 1980). Five fleshy-fruited plants are considered rare on Aldabra, represented by a few individuals only, and were therefore excluded from the analyses. For plant species, we use the nomenclature according to Friedmann (2011).

Seed dispersal interactions

We identified seed dispersal interactions on Aldabra using two complementary approaches, 'focused' and 'literature'. From these, we constructed interaction adjacency matrices to represent the networks, with one mutualist level in rows (e.g., frugivores) and the other in columns (e.g., plants), and where the absence or presence of interactions are depicted by zeros and ones in each cell, respectively. The focused interaction adjacency matrix and network were derived from field work on Aldabra during 2013–2015, while the literature adjacency matrix consisted of FSD interactions reported in the literature. The combination of both approaches represents the 'full' (observed) seed dispersal adjacency matrix (and network) for Aldabra, which is a subset of the possible adjacency matrix, given by the total number of potential frugivores (n = 13) and fleshy-fruited plants (n = 46; Fig. 2).

Field observations on FSD interactions were conducted between October 2013 and May 2014, and between January and October 2015. During the wet season of 2014–2015, monthly mean precipitation on Aldabra was not only below average, but was also more variable (102.7 ± 68.1), with two periods of higher than average precipitation, followed by two dry spells due to an intensive El Niño effect (SIF, unpubl. data). Precipitation on Aldabra is unevenly distributed across the atoll and the vegetation shows a strong response to precipitation events (Shekeine et al. 2015; Haverkamp et al. 2017). The low and irregular precipitation pattern experienced during the wet season of 2014–2015 limited the number of species and individual plants developing ripe fruit (H Richards, pers. comm.; WF, pers. obs.).

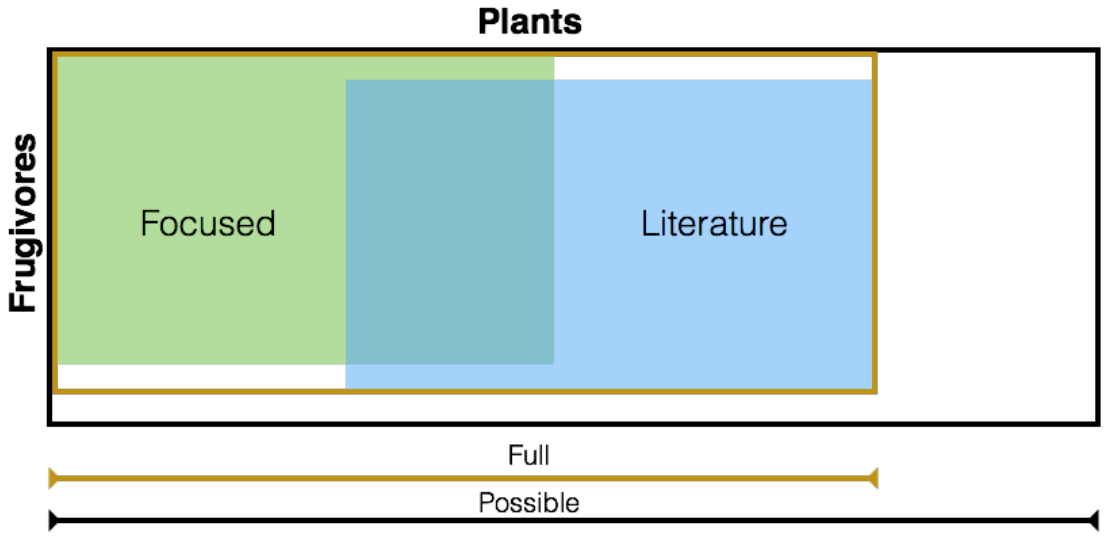

Figure 2: Layout of the observed (full) and possible plant–frugivore interaction adjacency matrices on Aldabra. The full matrix is given by the combination of the matrix derived from the focused and literature approaches (notice the overlap of interactions), and represents the Aldabra seed dispersal network. The possible matrix is given by the product of all the frugivores and fleshy-fruited plants that were expected to interact with each other.

Collecting FSD data of functionally diverse animals requires different approaches (e.g., Donatti et al. 2011). Therefore, we used four focused methods to construct a qualitative network: (i) focal observations; (ii) camera traps monitoring frugivore visitations at focal plants; (iii) scat analysis; and (iv) opportunistic observations. We collected data across the atoll mostly along long-term monitoring transects (set up by SIF for routine monitoring programmes) and occasionally in more open areas, with a main focus on Picard and Eastern Grande Terre due to easier accessibility (Fig. 1). The transects cover most vegetation types on all islands, thus maximising the probability of encountering FSD interactions of all fleshy-fruited plant species proportional to their abundance across the atoll. Opportunistic observations were made while doing other tasks such as transect walks looking for fruiting plants, installing camera traps and other activities. During the course of the study, we recorded the fruiting of 37 (target plants of the focused approach) of 46 possible fleshy-fruited plant species (80% of the fleshy-fruited plant community). Focal observations were performed on 23 plants from 17 species, camera traps were deployed on 53 plants from 20 species (there was species overlap between these methods). Scat sample collection was focused on Aldabra giant tortoises, and were collected along transects (10–20 scat samples per transect/visit). We recorded a

total of 71 focal observation hours (3 h ± 0.43 per species), 32,064 camera trap hours (1,603 h ± 1,935 per species), performed more than 400 h of opportunistic observations, and collected 431 scat samples.

We defined one seed dispersal event by a frugivore as: (i) fruits recorded to be swallowed or removed from a plant species during focal or opportunistic observations; (ii) fruit removal by an animal species recorded with camera traps or (iii) when a scat pile contained at least one seed of a plant species (Donatti et al. 2011). Seed dispersal events represent interactions between animal species *i* and plant species *j*, which are depicted as links between nodes in the network.

To overcome inherent sampling limitations of the focused FSD observations, we inferred links from the literature (e.g., Heleno et al. 2011) by surveying primary and grey sources reporting FSD interactions on Aldabra, which included: Grubb (1971); Benson & Penny (1971); Frith (1976); Hnatiuk (1978); Wickens (1979); Frith (1979); Hutson (2004); Brandis (2005).

Sampling completeness

Interaction sampling completeness (or robustness) of the focused approach was assessed by generating an accumulation curve with the number of unique interactions as a function of the total number of seed dispersal events sampled (Donatti et al. 2011). Following Jordano (2016) we used the package 'vegan' (Oksanen et al. 2017), implemented in R (R Core Team 2017), to extrapolate the species interaction accumulation curve, and estimated the number of species interactions expected according to different indices (Chao's, Bootstrap, Jack1, Jack2).

Network construction and structure

We constructed three SDNs for analyses: one each based on the focused approach, the literature approach, and the combined data (full network; see Fig. 2). We calculated general qualitative descriptors of the topology of the networks using the R-package 'bipartite' (Dormann et al. 2008) in R. The degree of nestedness was assessed with the NODF metric (Almeida-Neto & Ulrich 2011) implemented in the NeD program, with a null model based on proportional row and column totals (Strona et al. 2014). Modularity was evaluated using the software MODULAR

(Marquitti et al. 2014). The program was run using the M_B metric (Barber 2007) with the simulated annealing optimization algorithm (Guimerà & Amara 2005), and with the 'null model 2' (where the probability of each cell being occupied is the average of the probabilities of occupancy of its rows and columns; Bascompte et al. 2003). Significance levels of nestedness and modularity were tested against 100 randomly generated matrices. To visualise the structure of the full network, we followed García-Algarra et al. (2017) and ranked species based on *k*-core decomposition using the BipartGraph software (García-Santi & García-Algarra 2017). The *k*-core decomposition method classifies the nodes of the network into shells, which represent the different layers in the system, with the most connected nodes at the centre (inner shell). The shells are obtained by removing recursively vertices of degree smaller than *k*, until the degree of the remaining vertices is larger than or equal to *k* (Alvarez-Hamelin et al. 2005).

The ecological role of mutualists

In addition to analysing the general network topology, we also calculated network metrics at the trophic level, which describe properties of species in the network relative to other species in the same guild (i.e., within plants or within animals), and also at the species level. This was done using the full network only, because it represents all recorded plant–frugivore interactions on Aldabra, and thus a more complete picture of the ecological reality. We calculated the robustness to species extinctions, in a trophic level (e.g., plants) when species in the other trophic level (e.g., animals) were sequentially exterminated (Memmott et al. 2004). The robustness indicates the resistance of the system to the loss of species and has values of 0–1, with a value close to one indicating a slow decrease in the secondary extinction curve, and zero indicating a fast decrease in the curve. To determine the role of the different species in structuring the network, and our ability to preserve its functionality, we identified critical species in the network by using the package 'kcorebip' (García-Algarra & García-Santi 2017) in R, to calculate the three metrics *k*-radius, *k*-degree, and *k*-risk, which are based on the *k*-core decomposition. These metrics describe: (i) the network compactness, i.e., the distance of a node to the most generalist species in the partner guild; (ii) the combined quantity and quality of

interactions, i.e., information about the number of neighbours and how they are connected to the inner most shell; a measure of the centrality in the network), and (iii) the species' propensity to generate extinction cascades that fragment the network. To further understand the response of network structure to interactions decay and species extinction, we calculated the following metrics: normalised degree, closeness centrality and betweenness centrality (Martín González et al. 2010). These metrics allow us to determine the generalisation level of a given species, how direct the influence of a given species on others is (by measuring their distance to other species), and the ability of a given species to act as a connector between other species, respectively. These centrality measures range between 0 and 1, with values close to 1 indicating high generalisation (normalised degree) and a direct influence on all other species in the network by acting as a hub (closeness centrality), and values above zero indicating the relative importance of species as connectors in the network (betweenness centrality).

Results

Sampling completeness

Sampling completeness (robustness) for the focused approach varied from 48% to 82%, depending on the number of expected species interactions according to the different indices (Table 1; see Fig. 3 for accumulation curves). Moreover, with the focused approach, we recorded seven of 13 potential vertebrates and two crab seed dispersers interacting with 29 fleshy-fruited plants, of the 37 (78%) target species (i.e., that we observed fruiting on the atoll during the study period; 63% of all possible species). In the full interaction matrix, i.e., including data inferred from the literature, a total of 10 frugivores were recorded interacting with 37 fleshy-fruited plants, which increased our coverage to 80% of the possible fleshy-fruited plants.

Seed dispersal interactions

During focused FSD observations we recorded a total of 367 seed dispersal events and 78 unique pairwise interactions. From the literature, we inferred a total of 62 FSD interactions. Combining the two networks resulted in the full network having a

Table 1: Sampling robustness of the seed dispersal interactions derived from our focused approach according to different indices and their expected number of interactions. We recorded a total of 78 unique interactions using our focused approach.

Index	Expected interactions	±SE	Percent sampled
Chao	161.81	38.36	48%
Jack1	118.88	6.39	66%
Jack2	149.74	–	52%
Bootstrap	94.80	3.17	82%

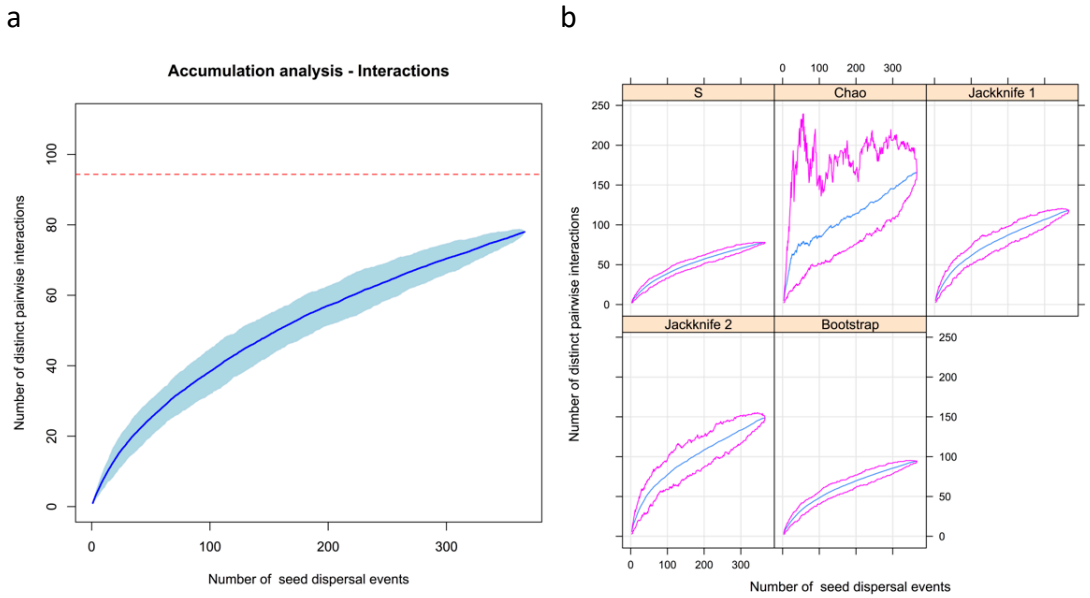

Figure 3: Interaction robustness accumulation curves for the focused approach-based seed dispersal network of Aldabra Atoll. The figure shows a) the interaction sampling robustness rarefaction curve, and b) the interaction sampling robustness accumulation curves based on the different indices.

total of 100 unique interactions (Fig. 4), and there was a 40% overlap between the interactions recorded for each network. Thirty-eight (~49%) of these interactions were unique to the focused approach, while 22 (~35%) were unique to the literature. The average number of links per species (degree) varied between 1.54 (literature approach) and 2.12 (focused approach; Table 2). In the full network, frugivores had a mean degree of 10, while plants had a mean of 2.8. The frugivores with the highest degree were the blue pigeons (26 links), followed by giant tortoises (20 links) and bulbuls (18 links). The most connected plants were *Flacourtia indica*, followed by

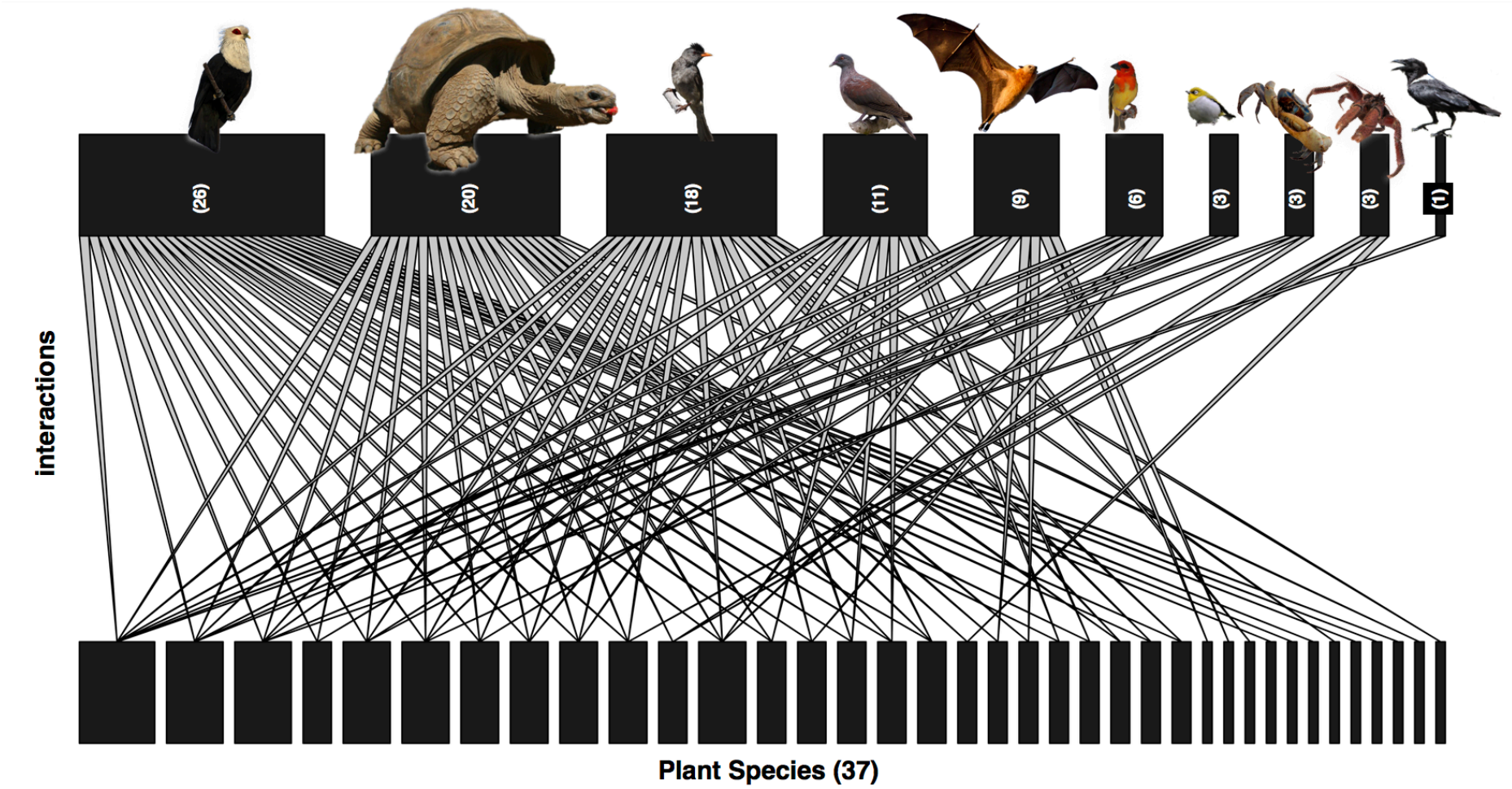

Figure 4: Seed dispersal network of Aldabra Atoll (bipartite representation). Frugivores are shown on top, while plants are shown at the bottom. The size of the boxes depicts the relative number of interactions (in parentheses for frugivores).

Ficus reflexa, *Apodytes dimidiata*, *Ficus lutea*, *Mystroxylon aethiopicum* and *Solanum aldabrense*, with 5–8 links per species.

Table 2: Description of the structural parameters of the seed dispersal network of Aldabra using three approaches: frugivory and seed dispersal events recorded during field focused observations, from the literature, and the combination of both.

Descriptor	Level	Focused network	Literature network	Full network
Frugivores	Network	9	9	10
Plants	Network	29	32	37
Connectance	Network	0.30	0.22	0.27
Nestedness (NODF)	Network	62.98*	33.33*	56.44*
Modularity (Q_B)	Network	0.30 NS	0.41NS	0.32NS
Modules	Network	1	1	1
Links per species	Network	2.05	1.54	2.12
Robustness	Frugivores	0.81	0.80	0.84
Robustness	Plants	0.70	0.63	0.69

NS = $p > 0.05$, * $p < 0.001$

Network structure

The three networks derived from the different approaches –focused, literature and full– exhibited similar structural properties (Table 2). All networks were highly asymmetrical (-0.57– -0.54), significantly nested, had a connectance range of 0.22–0.30, and consisted only of one module. The network derived from the literature approach had the lowest connectance and exhibited a somewhat less nested structure when compared to the other approaches (Table 2). Following the *k*-core decomposition, the full network was divided into four shells, with six frugivores and nine plants at its centre (4^{th}, inner most shell; Fig. 5). Moreover, both plant and frugivore levels showed high robustness, indicating high resistance to random secondary extinctions, with frugivores being more robust than plants. If species with higher degree were sequentially eliminated, however, robustness of the system decreased (Table 2).

The ecological role of key mutualists

Focusing on the full network, and reflecting their degree, blue pigeons were the most generalised seed dispersers in the network, followed by giant tortoises and bulbuls (Table 3). Frugivores had relatively similar scores of closeness centrality

(0.08–0.11), indicating similar distances between species in terms of number of links (calculated as the sum of the length of the shortest paths between the node and all other nodes). Blue pigeons, giant tortoises and bulbuls also served as main connectors in the network, indicated by relatively high scores of betweenness centrality and generalised degree. In addition, turtle-doves, white-eyes and land crabs also acted as connectors. For plants, *Flacourtia indica* had the highest normalised degree score, followed by *Apodytes dimidiata*, *Ficus reflexa*, *Ficus lutea*, *Mystroxylon aethiopicum* and *Solanum aldabrense* (all > 0.5; Table 4). Frugivores with the highest degree were most central (i.e., had higher *k*-degrees), and in case of these species becoming extinct, their disappearance is very likely to result in an extinction cascade in the network (i.e., had higher *k*-risk range; Table 3). Plants with a higher degree were also more central than those with fewer links, and the risk of their disappearance causing cascading extinctions did not seemed to be influenced by their degree (Table 4). In general, frugivores in the network were better connectors and more central than plants, and the integrity of the network was also more vulnerable to the extinction of animals than to that of plants. Like frugivores, plants had similar degrees of closeness centrality amongst themselves, and in general, plants that had a higher normalised degree also had higher betweenness centrality scores, with 62% of the plants acting as connectors (Table 4). Closeness centrality was not correlated with the normalised degree of the species (Spearman's rank correlation rho, $r = 0.18$, $p = 0.22$), but normalised degree and betweenness centrality were ($r = 0.72$, $p < 0.001$).

Discussion

In our study, we showed that the structure of the virtually intact Aldabra seed dispersal network follows the patterns observed in other seed dispersal networks. Moreover, the Aldabra SDN was robust to perturbations in general, and the data suggested that a specialist frugivore together with two partial frugivores drive the structure of the network.

Table 3: Centrality and *k*-magnitudes measures for frugivores in the seed dispersal network of Aldabra Atoll derived from the full network (combination of the focused and literature approaches).

ID	Species	Degree	*k*-shell	*k*-radius	*k*-degree	*k*-risk	ND	CC	BC
1	*Aelectroenas sganzii* (Blue pigeon)	26	4	1.00	13.71	33.04	0.70	0.11	0.24
2	*Aldabrachelys gigantea* (Aldabra giant tortoise)	20	4	1.00	11.16	18.04	0.54	0.11	0.24
3	*Hypsipetes madagascariensis* (Madagascan bulbul)	18	4	1.00	10.29	16.04	0.49	0.11	0.24
4	*Streptopelia picturata* (Turtle-dove)	11	4	1.89	6.13	10.04	0.30	0.10	0.08
5	*Pteropus aldabrensis* (Aldabra fruit bat)	9	4	2.119	5.36	11.04	0.24	0.10	0
6	*Foudia eminentissima* (Aldabra fody)	6	4	1.89	4.35	1.04	0.16	0.10	0
7	*Zosterops maderaspatana* (Aldabra white-eye)	3	3	2.339	2.35	0.03	0.08	0.10	0.08
8	*Cardisoma carnifex* (Land crab)	3	2	2.56	1.98	0.02	0.08	0.10	0.13
9	*Birgus latro* (Coconut crab)	3	2	3.00	1.25	0.02	0.08	0.08	0
10	*Corvus albus* (Pied crow)	1	1	2.78	0.60	0.01	0.03	0.09	0

Table 4: Centrality and *k*-magnitudes measures for plants in the seed dispersal network of Aldabra Atoll derived from the full network (combination of the focused and literature approaches).

ID	Species	Degree	*k*-shell	*k*-radius	*k*-degree	*k*-risk	ND	CC	BC
1	*Flacourtia indica*	8	4	1.00	5.35	3.04	0.8	0.03	0.12
2	*Ficus reflexa*	6	4	1.33	4.43	1.04	0.6	0.03	0.09
3	*Apodytes dimidiata*	6	4	1.67	4.32	4.04	0.6	0.03	0.05
4	*Ficus lutea*	5	4	1.33	4.00	0.04	0.3	0.03	0.09
5	*Mystroxylon aethiopicum*	5	4	1.33	4.00	0.04	0.5	0.03	0.09
6	*Solanum aldabrensis*	5	4	1.67	3.92	2.04	0.5	0.03	0.05
7	*Allophylus aldabricus*	4	4	1.67	3.53	0.04	0.4	0.03	0.04
8	*Scaevola taccada*	4	4	1.67	3.53	0.04	0.4	0.03	0.05
9	*Clerodendrum glabrum*	4	4	1.67	3.53	0.04	0.4	0.03	0.05
10	*Terminalia bovinii*	4	3	2.00	3.33	1.03	0.4	0.03	0.04
11	*Pandanus tectorius*	3	2	2.67	1.72	0.02	0.3	0.02	0
12	*Ficus rubra*	3	3	2.00	2.47	0.03	0.3	0.03	0.07
13	*Ochna ciliata*	3	3	2.00	2.53	0.03	0.3	0.03	0.04
14	*Polysphaeria multiflora*	3	3	2.00	2.53	0.03	0.3	0.03	0.01
15	*Scutia myrtina*	3	3	2.00	2.53	0.03	0.3	0.03	0.02
16	*Azima tetracantha*	3	3	2.00	2.53	0.03	0.3	0.03	0.04
17	*Aloe aldabrense*	3	3	2.00	3.00	0.03	0.3	0.03	0.04
18	*Pandanus aldabrensis*	2	2	2.67	1.33	0.02	0.2	0.02	0
19	*Cordia subcordata*	2	2	2.33	1.47	0.02	0.2	0.02	0.02
20	*Guettarda speciosa*	2	2	2.33	1.47	0.02	0.2	0.02	0.02
21	*Tarenna trichanta*	2	2	2.33	1.53	0.02	0.2	0.03	0.01
22	*Triainolepsis africana*	2	2	2.33	1.53	0.02	0.2	0.03	0.01
23	*Ehretia cymosa*	2	2	2.33	2.00	0.02	0.2	0.03	0.01

Table 4: (Cont.)

ID	Species	Degree	*k*-shell	*k*-radius	*k*-degree	*k*-risk	ND	CC	BC
24	*Phyllanthus casticum*	2	2	2.33	2.00	0.02	0.2	0.03	0.01
25	*Tarenna supra-axillaris*	2	2	2.33	2.00	0.02	0.2	0.03	0.01
26	*Sonneratia alba*	1	1	2.67	0.47	0.01	0.1	0.02	0
27	*Calophyllum inophyllum*	1	1	2.67	0.47	0.01	0.1	0.02	0
28	*Erythroxylum acrantum*	1	1	2.67	0.53	0.01	0.1	0.02	0
29	*Maillardia pendula*	1	1	2.67	1.00	0.01	0.1	0.03	0
30	*Margaritaria anomala*	1	1	2.67	1.00	0.01	0.1	0.03	0
31	*Premna obtufifolia*	1	1	2.67	1.00	0.01	0.1	0.03	0
32	*Asparagus umbellulatus*	1	1	2.67	1.00	0.01	0.1	0.02	0
33	*Sideroxylon inerme*	1	1	2.67	1.00	0.01	0.1	0.03	0
34	*Tricalysia ovalifolia*	1	1	2.67	1.00	0.01	0.1	0.03	0
35	*Canthium bibracteatum*	1	1	2.67	1.00	0.01	0.1	0.03	0
36	*Capparis cartilaginea*	1	1	2.67	1.00	0.01	0.1	0.02	0
37	*Cassytha filiformis*	1	1	2.67	1.00	0.01	0.1	0.02	0

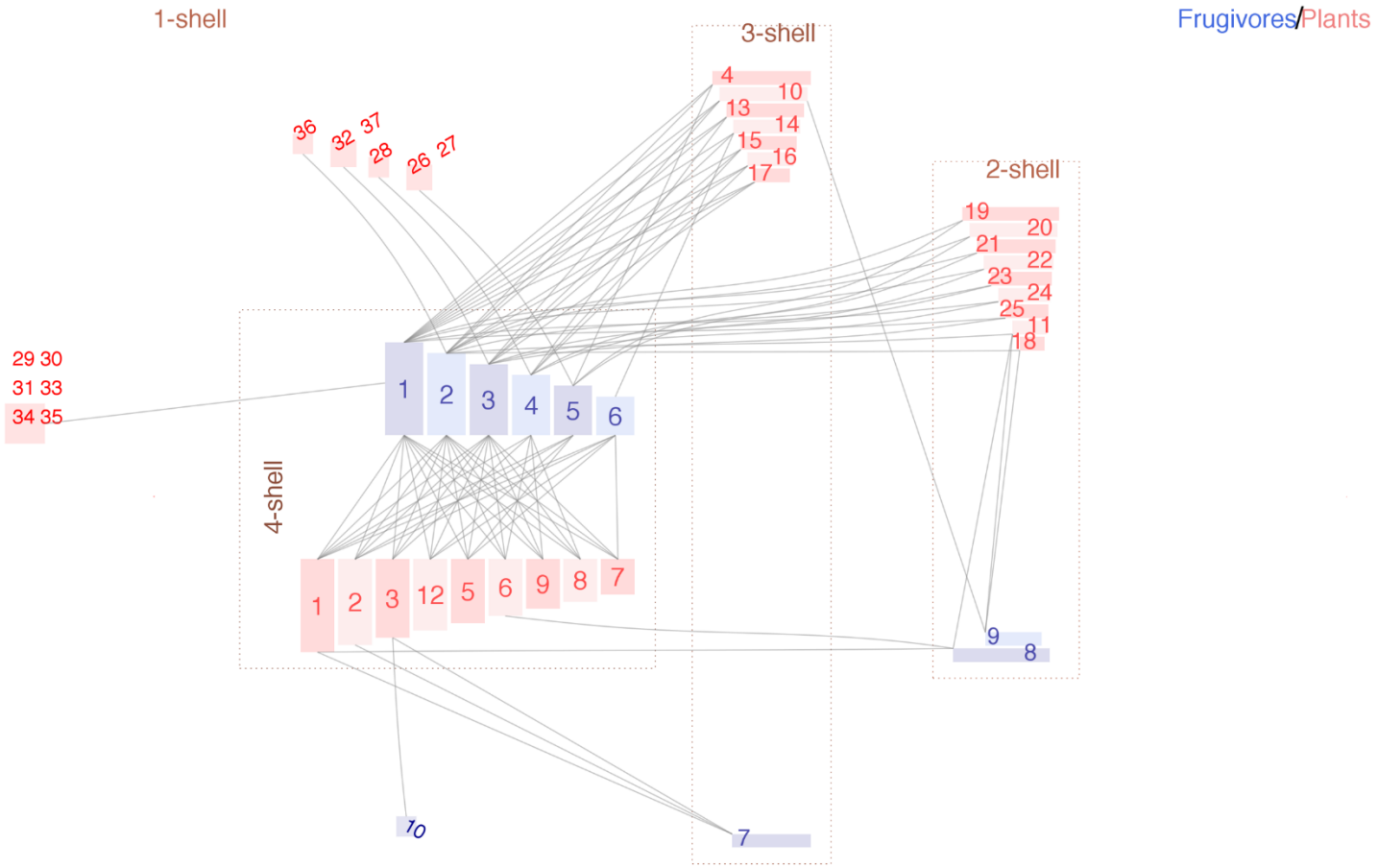

Figure 5: *k*-core decomposition of the Aldabra seed dispersal network. Plants are depicted in red, while frugivores are depicted in blue, and numbers indicate plants and frugivores as in Tables 3 and 4, respectively. The size of the nodes and colour shades improve visibility of individual links between species (i.e., they do not convey any information).

Network structure

Compared to other ecosystems where SDNs have been studied (e.g., Canary Islands, Gonzalez-Castro et al. 2012; Pantanal, Donatti et al. 2011), Aldabra is a very recently assembled ecosystem (Braithwaite et al. 1973) where there has been comparatively little time for co-evolution of traits between fruits and frugivores. However, the full seed dispersal network of Aldabra (from here on referred to as the seed dispersal network –SDN– of Aldabra) still maintains the invariant properties found in other mutualistic networks. Few species amassed most of the interactions in the network, especially for frugivores, making the network heterogeneous. The network was nested, made up of asymmetrical interactions, with the community well integrated around a central core of interactions, which contributes to the network displaying properties that imply functional redundancy, maintain network stability and promote biodiversity (Bascompte et al. 2003; Bastolla et al. 2009; Thébault & Fontaine 2010; Bascompte & Jordano 2014; but see Blüthgen et al. 2008; James et al. 2012). We found relatively low scores of *k*-radius amongst species (mean *k*-radius = 2.14 ± 0.55), and a high connectivity between the outer and inner shells, depicting a tightly compacted network (García-Algarra et al. 2017). Nested networks have a highly cohesive structure, which allows them to circumvent perturbations via alternative routes (Bascompte et al. 2003), and the asymmetrical pattern of interactions can provide pathways for network specialists to persist (Jordano 1987).

Although networks tend to be modular (Vázquez et al. 2009), the Aldabra SDN consisted of only one module. This is not surprising because of its size, as the presence of modularity in mutualistic networks is found in networks with over ~50 interacting species (Olesen et al. 2007). In agreement with this, we found relatively large mean value of *k*-degree (2.94 ± 2.75), where larger values are related to low modularity (when compared to other networks), and low connectivity within outer shells (García-Algarra et al. 2017). In modular networks, compartments are said to consist of a subset of species with convergent morphological traits (Bascompte & Jordano 2014). The fact that the Aldabra SDN is not modular is likely explained by its level of nestedness, size, and the functional groups represented by one or two frugivore species that have had little time to co-evolve with their plant partners.

Role of mutualists in the community

Overall, and considering the different metrics, frugivores were more central in the Aldabra SDN than plants. Reflecting its unimodular nature, there is an absence of hub species in the network, indicated by the low scores of closeness centrality. On the other hand, we found that about 60% of frugivores –and plants– acted as connectors (with frugivores acting as better connectors). Both closeness and betweenness centrality were lower when compared to the mean scores observed in pollination networks (Martín González et al. 2010). This, again, may be related to the unimodular nature of the network, and its size. Moreover, the inner shell of the network was made up of the most generalist species, and consisted of six vertebrate frugivores and nine fleshy-fruited plants (core species). Incidentally, the inner shell contained most of the best connector species in the network. Of the core species, frugivores had considerably higher *k*-degree scores, and thus were more central in the network.

Across different Neotropical bat- and bird-seed dispersal networks, only specialised frugivores reached the highest values of centrality measures (closeness and betweenness centrality), while values for partial and opportunistic frugivores are low (Mello et al. 2015). Moreover, centrality in these networks was best explained by diet specialisation, but not by body mass, indicating that specialised frugivores may play a central role in network and ecosystem structuring. Blue pigeons are obligate frugivores, and were the most generalised and central frugivore in the Aldabra SDN. However, fruit bats, which are the only other obligate frugivores, were not as prominent in the network. Rather, the partially frugivorous giant tortoises and bulbuls were the most central species following blue pigeons. Thus, on Aldabra, and contrary to bat- and bird-plant networks in the Neotropics, diet specialisation did not seem to influence centrality in the network. Instead, the species with higher degree and generalisation levels drove the structure of the Aldabra SDN, as also found in other network studies (Dunne et al. 2002; Martín González et al. 2010; James et al. 2012; Palacio et al. 2016).

Because of the virtually intact assemblage of plants and frugivores in our network, we expected the system to be robust to disturbances. Indeed, both plant and frugivore levels were robust to secondary extinctions when primary extinctions

occurred at random. However, if species with higher degree values were removed sequentially from the network, the robustness of the system was greatly reduced. In agreement with this, the extinction of species with a higher degree and overall centrality, made the integrity of the network more vulnerable (had higher *k*-risk scores), especially to the extinction of the largest vertebrate frugivores. This implies that these central species are particularly important for maintaining the integrity of the whole network (García-Algarra et al. 2017). Similarly, Vidal et al. (2014) found that the largest frugivores were at higher risk of extinction and were key elements in a seed dispersal network of the Atlantic forest in south-eastern Brazil. This is of special interest because, as in other places (Guimarães et al. 2008; Hansen & Galetti 2009; Heinen et al. 2017), most large frugivores are extinct in the islands of the south-western Indian Ocean. As a consequence, plant–frugivore networks in these islands are potentially unstable, with less connected plant species vulnerable to secondary extinctions (e.g., the disappearance of giant tortoises in the Mascarenes made some endemic plants vulnerable; Griffiths et al. 2011).

Key frugivores of Aldabra

In terms of centrality and generalisation in the network, blue pigeons were the most important species. They consume a large variety of fruits with different characteristics, and have the largest gape size amongst birds, ingesting fruits of up to ~15 mm in diameter (which allows them to potentially disperse 85% of fleshy-fruited plants on Aldabra). About 58% of Columbiformes are frugivorous, and they represent the largest percentage of frugivore birds after Passeriformes (Kissling et al. 2009). Pigeons are regarded as important seed dispersers in many ecosystems worldwide, especially for relatively large-seeded plants (e.g., Kitamura et al. 2002; McConkey et al. 2004; Wotton & Kelly 2012).

As with Galápagos giant tortoises (Heleno et al. 2013; Nogales et al. 2017), and Aldabra giant tortoises in Mauritius (Hansen et al. 2008), tortoises on Aldabra are important seed dispersers, being the second most generalised and most central species in the network. Different from the other frugivores in the network, they were able to ingest the largest fruits on the atoll, such as *Cordia subcordata* and *Pandanus aldabrense*, which (based on size) would allow them to potentially ingest

and disperse all species on the atoll. Moreover, they consumed non-fleshy fruits such as those of *Thespesia* spp. and immature ~50 mm large coconuts (*Cocos nucifera*; included for size perspective), and also include over 12 species of grasses and sedges (and their seeds; Fosberg & Renvoize 1980) in their diet. Thus, because they consume such a wide range of fruits (and seeds), their importance as seed dispersers, and particularly as connectors, is likely to be greater when all types of plants are considered.

Although they are considered partial frugivores and a major component of their diet is insects (Frith 1979), bulbuls consumed and dispersed the seeds of a large proportion of the fleshy-fruited plant community on Aldabra. Similarly, bulbuls disperse a large proportion of fleshy-fruited plants in other ecosystems (e.g., Kitamura et al. 2002; Linnebjerg et al. 2010). Furthermore, there was a high complementarity in the diet of bulbuls and pigeons on the atoll (62% overlap), similar to north-eastern Thailand, where fruit diet overlap between pigeons and bulbuls was 48% (Kitamura et al. 2002).

We were expecting fruit bats to be one of the most central frugivores in the network, because bats are known to consume and disperse the seeds of many species of plants, especially on islands (e.g., Cox et al. 1991; Florens et al. 2017). The fact that we recorded so few interactions of plants with bats, and that the reports from the literature were also low, may be linked to the nocturnal habit of the species. Potentially foraging bats are readily disturbed when a light source is pointed towards them, making foraging observations difficult. We made use of camera traps with night vision capabilities, which allowed us to record frugivory events by bats during the night. We placed our camera traps at a maximum height of 2.2 m, and although we recorded bats foraging at this height (e.g., on *Ficus* trees), it is possible that fruit bats prefer to forage at greater heights and/or in the canopy of the trees, which we did not cover due to logistical difficulties (the canopy on Aldabra can reach heights > 5 m, Fosberg & Renvoize 1980). In addition, bats on Aldabra appear to be highly mobile with no permanent or long-term roosts on Picard Island, so it was not possible to sample bat scat or ejectile in a systematic way. Another likely reason why we observed so few interactions of bats with plants is that the bat population on Aldabra is small, estimated at about 250 individuals (Hutson 2004), making the

detection of interactions much rarer compared to the other species (abundance influences the true occurrence of interactions as well as the occurrence of sampling effects; Vázquez et al. 2009). Nevertheless, they belong to the core of species in the network. After tortoises, they are the only other species capable of dispersing very large fruits, such as those of *Guettarda speciosa* or *Pandanus* spp.

Interestingly, two crab species formed part of the SDN of Aldabra. Crabs are often considered seed and seedling predators (Green et al. 1997; Capistrán-Barradas et al. 2006). However, as seen on Aldabra, crabs are also capable of dispersing hard-seeded plants and even large-seeded plants (Lee 1985; Wilde et al. 2004). On Aldabra, for example, coconut crabs drag *Pandanus* spp. fruits to consume the fibres surrounding the seed and later deposit them away from the mother plant. Moreover, coconut crabs have been observed climbing *Terminalia bovinii* trees to feed on the fruits (AJ Burt, pers. comm.). Like the latter, land crabs –which are connectors in the network– also drag *Pandanus tectorius* seeds away to consume the fibres, but we also observed them consuming the berries of *Solanum aldabrense* and *Flacourtia indica*, both with hard seeds that would likely survive gut passage. This behaviour has also been observed on Fanning Island in the central Pacific, where *Cardisoma carnifex* was found to disperse *Pandanus tectorius* an average of 7.3 m away from the parent plant (Lee 1985). It is likely that these crab species consume other fruits, especially berries, and those that fall on the ground. For example, coconut crabs on Christmas Island include fruits and seeds as a major part of their diet, in addition to animal material (Wilde et al. 2004). This is important because crabs are dominant organisms on islands, and probably arrive before large vertebrates do, establishing the possibility of seed dispersal in the absence of vertebrate frugivores. In addition, one unexplored aspect is the possibility of crabs as secondary dispersers, as they were often seen consuming the contents of tortoise dung, which include seeds. Whether crabs on Aldabra ingest seeds and pass them undamaged is unknown, but merits more attention.

Network construction & limitations

For the construction of the full seed dispersal network of Aldabra, we used the combination of two different approaches to gather information about FSD

interactions. In our focused approach, we relied on four different methodologies during two seasons of field observations. Although necessary to be able to detect FSD interactions by animals with different life histories and habits, this inevitably created possible sampling biases. According to the different indices and the species interactions curve, our focused approach covered between 48–82% of the expected interactions. These estimates assume that all links are possible in the network; however, there are forbidden links, that is, interactions that cannot occur due to, e.g., morphological constraints (Jordano 2016). Therefore, the actual interactions coverage is likely to be higher. The Chao's index had the lowest coverage value, and the highest standard error associated with the expected number of interactions. Nevertheless, our focused approach exhibited a rarefaction curve that reached 82% of the lower estimate of possible interactions, and the network showed the same structural properties as other seed dispersal networks reported in the literature, thus, we believe our sampling coverage is adequate to characterise the seed dispersal network of Aldabra.

To complement our dataset, and increase the coverage of plants sampled and of the number of FSD interactions, we added FSD information reported by various researchers on the atoll. This included peer-reviewed and non-peer-reviewed observations collected with various methods that could include biases in our dataset. For example, Frith (1979) noted that gizzard contents of Aldabra fodies indicated that fruits were consumed far more than what was indicated by records of feeding birds. Moreover, literature data of FSD in the Galápagos was biased towards birds (Heleno et al. 2011). In the case of Aldabra, both birds and tortoises were covered previously by several studies using different methods. In comparison, however, we know much less about the diet of invertebrates on the atoll. The literature-based network had lower connectance and was less nested than the focused network, which suggests that the literature data is inherently biased and should only be used in combination with other methods. However, adding data from the literature allowed us to cover 80% of the fleshy-fruited plant community on Aldabra, and increase the number of unique interactions from 78 to 100, highlighting the value of such information.

Differential seed dispersal efficiency

The seed dispersal services that frugivores provide to plants are not equivalent for the different species. For example, frugivores differ in terms of the quantity (e.g., number of seeds) and the quality (e.g., handling behaviour) of seeds dispersed; the so-called seed dispersal efficiency (Schupp et al. 2010). Consequently, when considering the interactions given by a qualitative network (e.g., for conservation or restoration purposes; in the absence of quantitative data), these must be interpreted together with the biology of the species involved. For example, giant tortoises and birds differ in their size (and gape size), movement ecology, and the treatment they give to the fruits and the seeds they consume. In addition to ingesting the fruits, birds can regurgitate them, and this may depend on the plant species and type of fruit. Furthermore, as birds, they are volant and may travel and disperse between islands (movement of tortoises between islands can be considered rare). Birds, however, are more constrained in terms of the capabilities of long distance dispersal when compared to tortoises because they have much shorter mean seed gut retention time; <260 min for pigeons (e.g., Meehan et al. 2003) and 15 min for bulbuls (e.g., Linnebjerg et al. 2010). Bulbuls are considered territorial and travel mostly within islands while blue pigeons and turtle doves are known to commute between islands (WF, pers. obs.). Thus, we expect birds in general to disperse seeds at medium distances within islands, and for blue pigeons and turtle doves to be important vectors for seed dispersal between islands (especially for small-seeded plants, albeit at a low frequency). Tortoises on Aldabra, on the other hand, have an average seed gut retention time of 15 days and can hold seeds up to 33 days (Falcón et al. Chapter 3), all seeds recorded in their dung passed undamaged, and seed load is often high (i.e., high propagule pressure), and deposited in a dung pile, which is rich in nutrients and may aid plants to germinate. Indeed, 28 species of plants were reported to germinate from tortoise dung collected in the field on Aldabra (Hnatiuk 1978). This, together with the movement ecology of tortoises (Baxter 2015), and the fact that tortoises can ingest fruits of a wide range of sizes indicates that tortoises may provide intra-island long-distance dispersal services to plants more frequently than their bird counterparts.

Conservation and management implications on Aldabra

Because Aldabra is a strict nature reserve and a UNESCO World Heritage Site, direct negative anthropogenic impacts are minimal. Reflecting this, populations of birds, tortoises, and crabs are currently considered stable (Turnbull et al. 2015; van de Crommenacker et al. 2016; SIF, unpubl. data). As a coral atoll, however, Aldabra is especially at risk of being negatively impacted by sea level rise. Moreover, climate change is expected to affect fruit production and seed dispersal of plants across the world (McConkey et al. 2012), with islands being at higher risk than the continents (Kaiser-Bunbury et al. 2010). Indeed, the occurrence of droughts on Aldabra has been increasing over the years, and vegetation productivity of some habitats on the atoll is especially sensitive to these changes in precipitation (Shekeine et al. 2015; Haverkamp et al. 2017). Specially at risk of being negatively affected by droughts are mixed scrub areas on the atoll (Haverkamp et al. 2017), which harbour the majority, if not all, of the fleshy-fruited plants. Given the intricate relationship between plants and their frugivores, and the ecological implications of seed dispersal, the continued monitoring of plant phenology and frugivore activity is essential to guide and inform management actions.

If the monitoring of seed dispersal interactions is to be implemented, there are several recommendations that follow from our experience on the atoll. In terms of the monitoring methods employed, performing focal observation was the most time consuming one, with little reward when compared to the other methodologies. Given the personnel and time limitations to do ecological monitoring on Aldabra, we recommend using a combination of opportunistic observations, camera traps, and faecal analyses.

Opportunistic observations of frugivory and seed dispersal can be easily incorporated to the bird and tortoise monitoring protocols that are currently being carried out on the atoll. These are performed between 07:00–09:00, which is when birds and tortoises are actively feeding. The adoption of monitoring tools such as CyberTracker (www.cybertracker.org) implemented in Trimble® would make the simultaneous monitoring of birds, tortoises, and seed dispersal interactions easier and more efficient (but paper forms should always be at hand in case of equipment failures). Moreover, it can serve to record data from the other methodologies.

Similar to opportunistic observations, the collection of faecal samples can be easily incorporated into the monitoring protocols. For example, in the case of tortoises, faecal samples can be collected from the monitoring transects of the way back to camp, once the morning monitoring period has ended. Tortoise scat can be put in separate paper bags and stored in dry conditions indefinitely. In the case of birds, faecal samples may be collected when performing mist netting, and stored individually in vials with ethanol for later analysis. The identification of seeds will require experience and/or a reference collection, and is the most time-consuming part of this method.

The use of camera traps is another efficient and low time-consuming method, in terms of implementation. There are different models of camera traps available, and personnel should familiarise themselves with the capabilities and limitations of the model at hand. Depending on the conditions, such as wind or coconut crab activity (for some reason they are attracted to camera traps when set at low heights), the camera traps used in this study lasted from days to over a month active in the field. To maximise battery life and SD card recording time, while maximising detection rates, experience is needed to determine the trade-offs between sensor sensitivity, and avoiding factors other than frugivores triggering the camera. For example, wind is more likely to trigger the cameras in coastal areas than in the interior of the atoll. Therefore, the sensitivity should usually be set to a lower level to avoid vegetation movement triggering the cameras. The data review may take some time, and we recommend tabulating the data soon after the cameras are recovered. One factor that made the review of the videos recorded more efficient was the simultaneous use of photos and videos when the cameras were triggered. By using this function, the personnel can inspect photos for presence of frugivores, and identify which videos to view. Preliminary analysis with a subset of the data collected here indicated that the detection rate of true frugivore activity was high, with omission rates virtually absent. Thus, reviewing photos for presence of frugivores would avoid having to review all the videos recorded (which can be hundreds if the cameras are constantly triggered by wind).

Using this combination of methods is a cost-effective way of monitoring seed dispersal interactions on Aldabra Atoll given the existing limitations in working on

such an isolated place. By integrating the monitoring of seed dispersal to the general monitoring scheme, not only can get a clearer picture of the plant–frugivore interactions that occur in the atoll, but we can also gain insights into the quantitative nature of the network, and the space-time dynamics affecting these interactions, such as differences between islands and seasonality. The prospects for furthering our understanding of seed dispersal interactions by using the intact seed dispersal network of Aldabra Atoll as a model system are encouraging.

Conservation and management implications on the SWIO

Most islands in the southwestern Indian Ocean have seen their frugivores, especially large-bodied ones, go extinct, leaving behind plants without their mutualist partners and prone to secondary extinctions. Because these islands had similar plant–frugivore assemblages as on Aldabra, the metrics ranking the importance of frugivores provided in this study can be used to inform reintroduction efforts aimed at rebuilding and maintaining the larger component of the seed dispersal networks.

Different conservation organisations have begun rewilding programs, that is, introducing analog species to extinct ones to restore the ecosystem functions that were lost. One example of this is the introduction of Aldabra giant tortoises, considered an ecosystem engineer, to islands in the Mascarenes to restore the function left behind by the extinct *Cylindrapsis* giant tortoises (Hansen et al. 2010; Griffiths et al. 2010) . The information derived from the Aldabra SDN (e.g., high centrality and *k*-risk) together with information about the biology of tortoises such as gape size, seed gut retention time, and their movement ecology indicate that Aldabra giant tortoises would be excellent candidates for the re-establishment of seed dispersal mutualisms, especially for large-fruited species. Indeed, studies have shown that Aldabra giant tortoises effectively disperse the seeds of different native species of plants where they have been introduced (Griffiths et al. 2010), including large-seeded species such as an ebony species in Mauritius (*Diospyros egrettarum*). Another option in addition to –or instead of– tortoises would be an analogue to blue pigeons and/or bulbuls (e.g., in Rodrigues, where both endemic forms went extinct). Unlike giant tortoises, these species are volant, and have dietary preferences, seed

gut retention times, fruit and seed treatment behaviours, and potential movement ecologies that are complementary to that of tortoises. Similarly, plants like *Flacourtia indica*, *Ficus reflexa*, and *Apodytes dimidiata* can be considered for propagation programs, with the aim of supporting as many frugivores as possible. To further use the information acquired from the seed dispersal network, a quantitative framework for assigning potential interactions is needed, and should consider the functional trait space of plants and their corresponding seed dispersers.

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3

LARGER DOESN'T MEAN LONGER: NEITHER BODY SIZE NOR SEED SIZE AFFECT THE GUT RETENTION TIMES OF ALDABRA GIANT TORTOISES

CHAPTER 3

Larger Doesn't Mean Longer: Neither Body Size nor Seed Size Affect the Gut Retention Times of Aldabra Giant Tortoises

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Abstract

Seed dispersal through endozoochory is a critical ecosystem function worldwide. Seed gut retention time (GRT; the time seeds are retained in the digestive tract) is an important part of the qualitative component of the seed dispersal effectiveness framework. GRT is a major determinant of when and how far away seeds are dispersed, aiding seeds in escaping predation in space as well as in time. In this study, we examined whether the size of the disperser and/or the size of the ingested seeds affect the GRT in Aldabra giant tortoises (*Aldabrachelys gigantea*) on Aldabra Atoll, Seychelles, where they are endemic. We selected tortoises of varying body mass (range 0.6–104.0 kg; mean = 48.6 kg ± 27.2 SD) and fed them different-sized artificial seeds (2, 4.5, and 10 mm). Tortoises defecated the first seeds a mean of 12.0 (± 2.7) days after ingestion, and the last seeds 20.4 (± 6.0) days after ingestion. Mean GRT was 14.6 (± 3.7) days. We show that neither tortoise body size nor seed size had an effect on the patterns and time of defecation. We discuss the relevance of our result for seed dispersal and for rewilding projects that use Aldabra giant tortoises as substitute species for extinct giant tortoises on other oceanic islands.

Key words: *Aldabra Atoll;* Aldabrachelys gigantea*; Chelonian; Mass; Passage time; Seed dispersal*

Resumen

La dispersión de semillas por medio de la endozoocoría es mundialmente una función crítica para los ecosistemas. El tiempo de retención de semillas en el tracto digestivo (TRD) es una parte importante del componente cualitativo del marco operativo del concepto de la efectividad de dispersión de semillas. Es un determinante importante en cuanto a cuán lejos las semillas son dispersadas desde la planta madre, y potencialmente ayuda a las semillas a escapar la depredación en el tiempo y el espacio. En este estudio, examinamos si el tamaño del dispersor de semillas y/o el tamaño de las semillas dispersadas afectan el TRD en las tortugas gigantes de Aldabra (*Aldabrachelys gigantea*). Seleccionamos tortugas con masa corporal variada (rango: 0.6–104.0 kg; media = 48.6 kg ± 27.2 desviación típica, DT), y las alimentamos con semillas artificiales de distintos tamaños (2, 4.5 y 10 mm) en el Atolón de Aldabra, Seychelles, de donde son endémicas. En promedio, las tortugas defecaron las primeras semillas 12.0 (± 2.7) días luego de ser ingeridas, y las últimas semillas fueron defecadas un promedio de 20.4 (± 6.0) días luego de ser ingeridas. El TRD promedio fue de 14.6 (± 3.7) días. Nuestros resultados demuestran que las tortugas gigantes de Aldabra tienen TRDs relativamente largos, y que ni el tamaño de las tortugas ni el tamaño de las semillas afectan los patrones y tiempos de defecación. Discutimos la relevancia de estos resultados para la ecología de dispersión de semillas y para los proyectos de restauración que usan las tortugas gigantes de Aldabra como especies substitutas a aquellas tortugas gigantes que se han extinto en otras islas oceánicas.

Introduction

Animal-mediated seed dispersal is an important ecosystem function that determines the structuring of plant populations and biodiversity, and has profound ecological and evolutionary implications (Howe & Smallwood 1982; Stoner & Henry 2008). Endozoochory, which is the dispersal of seeds ingested by animals, is the most common form of animal-mediated seed dispersal, with as many as 75% of plants in tropical forests depending on animals to disperse their seeds (Howe & Smallwood 1982). A major goal of seed dispersal ecology is to identify not only which seeds are being dispersed by what frugivore, but the proportion of seeds dispersed by a given animal that will germinate, and ultimately grow into a mature plants—the so-called seed dispersal efficiency (SDE) concept (Schupp 1993; Schupp et al. 2010).

Gut retention time (GRT; the time seeds are retained in the digestive tract) is one measure of SDE. Retention time in the gut of frugivores may determine the distance of dispersal and the structure of the seed rain shadow. The treatment of seeds in the gut can also affect seed viability (Schupp 1993; Traveset 1998). Moreover, temporal retention of seeds and subsequent deposition away from the mother plants may aid seeds in escaping predation, affect their germination and determine the outcome of seedlings as adult recruits (Connel 1971; Guzmán & Stevenson 2011; Janzen 1970). Intraspecific differences in frugivore GRTs due to varying body size, as well as in retention times for seeds of different sizes can influence seed deposition patterns. Understanding the relationship between frugivore mass and/or seed size and the GRT of a given frugivore species therefore enables more accurate predictions concerning the shape and size of the seed shadow and the subsequent seedling recruitment probability.

Aldabra giant tortoises (*Aldabrachelys gigantea*) are considered ecosystem engineers, regulating plant populations through trampling, herbivory and seed dispersal (Gibbs et al. 2010; Hansen et al. 2010; Hnatiuk 1978). Moreover, they are used as a key species in rewilding projects on other oceanic islands where they are functionally replacing recently extinct endemic giant tortoises (Griffiths et al. 2010; Hansen et al. 2010). In this study, we conducted *in situ* GRT experiments on Aldabra giant tortoises of a broad size range by feeding them artificial seeds of different sizes. All else being equal, larger tortoises have longer digestive tracts (Hatt et al.

2002) and larger, heavier, seeds are expected to travel more slowly through the digestive tract (e.g., Holbrook & Smith 2000). We thus expected that the GRTs of larger seeds fed to tortoises with greater body mass would be longer, and vice versa for smaller seeds fed to smaller tortoises. Moreover, we expected to find an interaction between tortoise mass and seed size, with tortoise mass increasing the slope of the relationship between seed size and GRT.

Methods

Study Site and Study Animal

Aldabra Atoll, Republic of Seychelles, is a raised coral atoll (155 km^2) in the southwestern Indian Ocean, composed of four main islands enclosing a central lagoon and several islets, and is managed by the Seychelles Islands Foundation. The atoll has a tropical climate with a wet (November–April) and dry season (May–October). Because it supports an almost intact native fauna and flora with very few invasive species, Aldabra was declared a UNESCO World Heritage site in 1982. The study was conducted on Picard Island, where the research station is located (9°24'4.46"S, 46°12'22.42"E; datum = WGS84).

Aldabra giant tortoises (*A. gigantea* Schweigger 1812; Fig. 1a) are endemic to Aldabra. Their population is estimated to be around 100,000 individuals (Bourn et al. 1999), and is considered stable (Turnbull et al. 2015). Aldabra giant tortoises show varying degrees of sexual dimorphism across the atoll, with males being considerably larger than females in the west of the atoll, to almost no sexual differences to the east of the atoll (Turnbull et al. 2015). Tortoise size varies from 0.05 kg hatchlings to as much as 84 kg female and 125 kg male adults in the wild on Aldabra.

Gut retention time experiment

To determine whether the size of tortoises or the size of seeds have an effect on the GRT, we selected 14 tortoises with body mass of 0.2–104.0 kg (mean = 48.6 ± 27.2; see Table 1) and fed them with artificial seeds (plastic beads; e.g., Willson 1989) of three different diameters and mass: 2 mm (0.03 g), 4.5 mm (0.09 g) and 10 mm (1.20 g; which are within the size-range of seeds dispersed by tortoises on Aldabra Atoll). As in other GRT studies, we assume that plastic beads are a suitable

proxy for seeds in GRT studies. For example, Sadeghayobi et al. (2011) tested simultaneously plastic beads and natural seeds as passage time markers and found no differences in GRT or excretion patterns in terms of passage marker size.

The tortoises were kept in enclosures under natural conditions and had access to leaves of woody vegetation of known food plants on the atoll and to water *ad libitum* during the trials. Three trials with three different sets of tortoises were conducted. Fifty beads of 2.5 mm and 4.5 mm each, and 25 beads of 10 mm were fed to the tortoises in rice balls with tomato paste (to encourage consumption). Each tortoise was fed beads of a single color, allowing scats to be assigned to specific tortoises, and all tortoises per trial were fed beads within two days. The juvenile tortoise was kept in a separate, smaller enclosure and fed only 12 of each of the 2 mm and 4.5 mm beads. Scat was sampled twice a day and searched for beads, until seven days after the last scat with beads was found. After sieving all scats, we recovered a mean of 80% of beads per tortoise (± 10%; Table 1), which is a similar recovered percentage as in other studies (Willson 1989; Sadeghayobi et al. 2011). See Figure 1b–f for a depiction of the process.

Statistical analyses

We analyzed the data with R v. 3.3.3 (R Core Team 2017), and visualized it with package 'ggplot2' (Wickham 2016). We reported the time (days) when the first and last beads were recovered, respectively, and calculated the mean GRT as the mean number of days for the beads to be defecated. We report all values with standard deviations (SD). To examine whether tortoise size and/or seed size affect GRT, we used package 'lme4' (Bates et al. 2015), and constructed a generalized linear mixed model. Because we counted the number of days each artificial seed spent in the gut, and after testing different probability distributions with our data, we specified the Poisson distribution in the model. Specifically, we tested whether time (GRT in days for each bead), tortoise mass, seed size, and the interaction between tortoise mass and seed size affected the number of beads recovered each day. To account for individual variability and differences in conditions between trials, we added tortoise ID and trial number as random effects.

Figure 1: An Aldabra giant tortoise on Aldabra Atoll (a), and the process undertaken to perform the seed gut retention time experiments (b–f). Tortoises were held in enclosures during the feeding experiments (b) and selected tortoises where weighted (c). Different sized artificial seeds were fed embedded in rice balls with tomato sauce to the tortoises (d), which were later defecated (e) and counted each day after sieving fecal matter (f).

Results

Tortoises deposited the first beads a mean of 12.0 days (± 2.7 SD), and the last beads 20.4 days (± 6.0; Table 1), and there was considerable variation between individuals (Fig. 2). In general, defecation patterns of artificial seeds by tortoises showed a steep increase around 12 days after ingestion, with the highest proportion of artificial seeds defecated around 15 days after ingestion, followed by a steep decrease after

18 days, with a long tail of up to 33 days (Fig. 3). The mean GRT was 14.6 days (± 3.7); 14.7 days (± 3.7) for 2 mm beads, 14.6 days (± 3.9) for 4.5 mm beads, and 14.3 days (± 3.6) for 10 mm beads (Fig. 3). We found no relationship between the proportion of beads recovered, and the days elapsed until the first and last beads were recovered, nor with mean GRT.

Table 1: Sex mass and size of tortoises used for the gut retention time (GRT) trials, times of defecation, and the proportion of beads recovered per individual. 'F' stands for female, 'M' stands for male and 'J' stands for juvenile.

Trial	Tortoise ID	Sex	Mass (kg)	1st beads (day)	Mean GRT (days)	±SD GRT (days)	Last beads (day)	Prop. of beads rec.
1	JUV	J	0.2	16	17.3	1.8	21	1.0
2	JAW	F	18.0	14	18.1	2.8	23	0.89
2	JOP	F	35.0	10	17.4	3.3	33	0.85
3	WIL	F	35.0	10	10.7	1.9	22	0.83
2	BDO	F	39.0	17	20.3	2.5	28	0.89
3	BEL	F	39.0	11	11.6	0.8	13	0.73
3	AIV	F	46.0	11	15.6	1.9	18	0.79
2	AJV	M	46.0	9	12.1	3.0	26	0.95
3	UNM	M	48.0	11	12.5	1.1	14	0.76
2	BGA	F	48.5	11	13.8	2.5	24	0.91
3	CFK	F	61.0	12	16.0	1.1	17	0.65
3	AHL	F	64.0	8	8.6	0.7	12	0.80
3	LDX	M	97.0	13	14.2	0.6	16	0.89
2	PWH	M	104.0	15	16.8	1.1	19	0.92

According to the statistical model, neither tortoise body mass, seed size, nor their interaction, had an effect on GRT ($p > 0.34$; Table 2). Instead of body mass, carapace size has been used as an index of size (e.g., Sadeghayobi et al. 2011). Fitting the model with third vertebral scute width (which is related to mass in Aldabra giant tortoises) resulted in equally non-significant results.

Table 2: Results of the generalized linear mixed effect model evaluating whether tortoise mass and/or seed size (and their interaction) affect the gut retention time of Aldabra giant tortoises.

Fixed effects	Estimate	Std. error	z value	*p*
intercept	2.720	0.130	20.953	<0.001
mass	-0.001	0.002	-0.462	0.644
bead size 4.5 mm	0.006	0.035	0.179	0.858
bead size 10 mm	-0.040	0.043	-0.948	0.343
mass:bead size 4.5 mm	0.001	0.001	0.179	0.858

Discussion

Our results demonstrate that, within the size-range tested, neither tortoise size nor seed size affect GRT of Aldabra giant tortoises. The mean GRTs found in this study are within the range of GRTs found for Aldabra giant tortoises in other studies (mean GRT: 17–21 days [70–100 kg], Hansen et al. 2008; 13 days for sub-adults [20–30 kg] and 18 days for adults [75–180 kg], Waibel et al. 2013), and longer than those reported for the similarly-sized Galápagos giant tortoises (*Chelonoidis nigra*, mean GRT: 8–9 days for juveniles [7–38 kg] and 9–12 days for adults [100–210 kg], Hatt et al. 2002).

Some studies on Aldabra and Galápagos giant tortoises have found an effect of body mass on GRT. Waibel et al. (2013) found that sub-adult Aldabra giant tortoises had a shorter GRT than adults of fruit seeds, and Hatt et al. (2002) found that GRT of *n*-alkalene particles was shorter for smaller Galápagos giant tortoises. However, contrary to our expectations, we found no effects of body mass on tortoise GRT. Even the juvenile individual exhibited a mean GRT similar to that of adult tortoises (mean GRT of 17.3 days after ingestion vs. 14.4 ± 3.3 days for adults). Bjorndal & Bolten (1992) reported for the river turtle *Pseudemys nelsoni* that even though adults were 250 times larger than hatchlings in terms of body mass, their GRT was only 1.4 times longer. Several other studies have also failed to find a relationship between body mass and GRT in chelonians. For example, in a study of red- and yellow-footed tortoises (*Chelonoidis carbonaria* and *C. denticulata*, respectively) which were fed wild fruit species, Bjorndal (1989) showed that body mass did not influence GRT. Using artificial seeds (plastic beads), Sadeghayobi et al. (2011) found that body mass did not influence the GRT of Galápagos giant tortoises, either. In terms of seed size, Varela & Bucher (2002) found no effect of seed size of

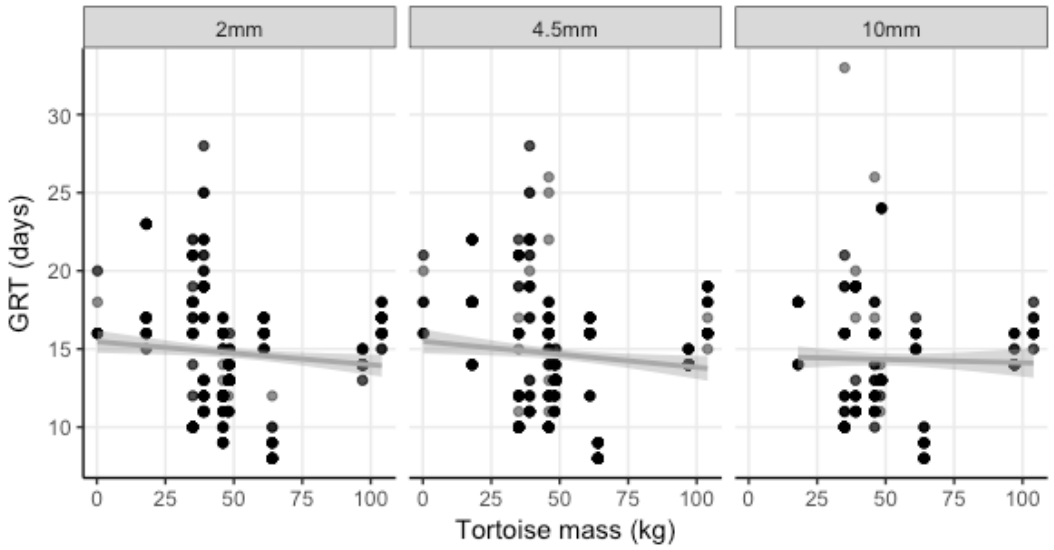

Figure 2: Gut retention times (GRT) of Aldabra giant tortoises in relation to their mass, and according to seed size (plastic beads; indicated in the top panel). Darker shading of points indicates a higher frequency of observations. Lines denote the relationship between mass and GRT (not significant).

wild plants on GRT of Chaco tortoises (*Chelonoidis chilensis*). Moreover, Braun & Brooks (1987) found that when the relatively small box turtle (*Terrapene carolina*) was fed fruits of common wild plant species, seed size did not influence GRT, but it did influence the percentage of seeds that passed intact, with larger seeds being more likely to be defecated.

In the different studies conducted on Aldabra and Galápagos giant tortoises, diet was consistent within experiments, but varied between studies. In the studies that found no effect of giant tortoise body size on GRT, animals had access to woody vegetation as food plants (this study) and fruits (Sadeghayobi et al. 2011), whereas in studies that found an effect of giant tortoise size on GRT, food plants consisted of grasses (mainly *Cynodon dactylon*; Waibel et al. 2013), or a mixture of rye grass (*Lolium perenne*), fruits and vegetables (Hatt et al. 2002). It is possible that these differences in diets as well as other factors (see below) led to the different results.

The effect of body mass and/or seed size may vary within and between species due to other factors known to affect GRTs in chelonians. For example, GRT can vary across seasons in habitats with wet and dry periods, with faster passage time during wet periods (e.g., in Aldabra giant tortoises; Coe et al. 1979). Moreover, in general, temperature plays a role in regulating GRT, leading to

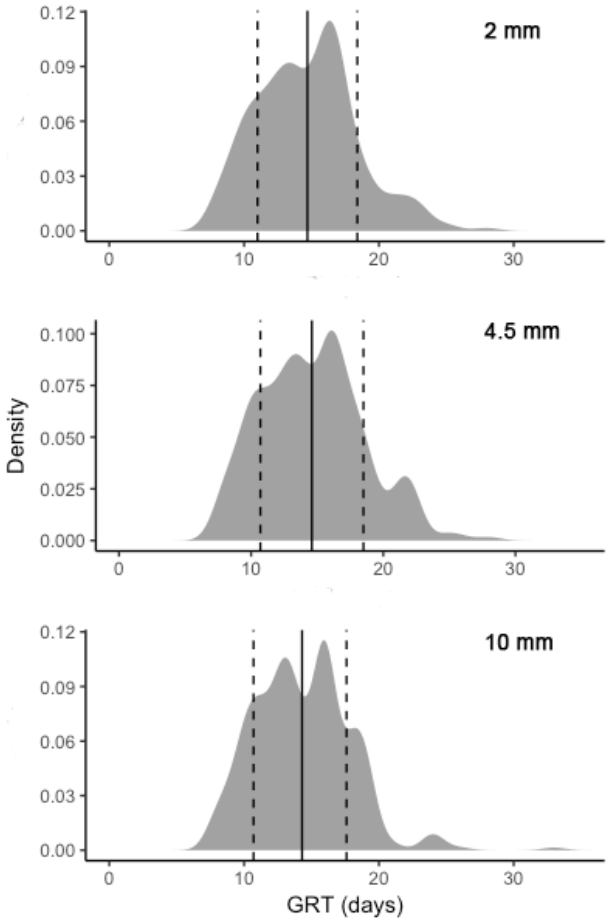

Figure 3: Density distribution of gut retention time (GRT; days until defecation) per artificial seed size (plastic beads). Means are shown with solid lines and their standard deviations with stippled lines.

faster passage with increasing temperature (Sadeghayobi et al. 2011). In addition, GRT depends strongly on plant species, amount of fruits consumed, and overall diet (Bjorndal 1989; Stone & Moll 2006).

Aldabra giant tortoises are currently being used in several rewilding projects as taxon substitutes for recently extinct endemic giant tortoises, with seed dispersal being one of the most common extinct interactions that practitioners aim to resurrect to restore ecosystem functions (Griffiths et al. 2011; Hansen et al. 2008; Kaiser-Bunbury et al. 2010). Giant tortoises are especially important as seed dispersers because they can ingest a wide range of fruit sizes and can move long distances, thus serving as megafaunal seed dispersers (Hansen et al. 2010; Hansen &

Galetti 2009). In general, despite the long GRT of Aldabra giant tortoises, the effect of gut passage on seeds is neutral or in some instances improves the germination rate of seeds and/or the growth of seedlings (Andriantsaralaza et al. 2013; Griffiths et al. 2011; Hnatiuk 1978; Waibel et al. 2013). Our results suggest that both small and large tortoises are equally capable of retaining small and large seeds in their guts for 2–4 weeks, and thus, from a seed dispersal point of view, similarly useful in rewilding projects.

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4

PATTERNS OF ACTIVITY AND BODY TEMPERATURE OF ALDABRA GIANT TORTOISES IN RELATION TO ENVIRONMENTAL TEMPERATURE

CHAPTER 4

Patterns of activity and body temperature of Aldabra giant tortoises in relation to environmental temperature

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Abstract

We studied the temperature relations of wild and zoo Aldabra giant tortoises (*Aldabrachelys gigantea*) focusing on: 1) the relationship between environmental temperature and tortoise activity patterns (n = 8 wild individuals), and 2) on tortoise body temperature fluctuations, including how their core and external body temperatures vary in relation to different environmental temperature ranges (seasons; n = 4 wild, and n = 5 zoo individuals). In addition, we surveyed the literature to review the effect of body mass on core body temperature range in relation to environmental temperature in the Testudinidae. Diurnal activity of tortoises was bimodally distributed, and influenced by environmental temperature and season. The mean air temperature at which activity is maximised was 27.9˚C, with a range of 25.8–31.7˚C. Furthermore, air temperature explained changes in the core body temperature better than did mass, and only during the coldest trial did tortoises with higher mass showed more stable temperatures. Our results, together with the overall Testudinidae overview, suggest that, once variation in environmental temperature has been taken into account, there is little effect of mass on the temperature stability of tortoises. Moreover, the presence of thermal inertia in an individual tortoise depends on the environmental temperatures, and we found no evidence for inertial homeothermy. Finally, patterns of core and external body temperatures in comparison to environmental temperatures suggest that Aldabra giant tortoises act as mixed conformer-regulators. Our study provides a baseline to manage the thermal environment of wild and rewilded populations of an important island ecosystem engineer species in an era of climate change.

Key words: *Aldabra*, *giant tortoise*, *ectotherm*, *Testudinidae*, *thermoregulation*

Resumen

En este artículo, estudiamos las relaciones térmicas de las tortugas gigantes de Aldabra (*Aldabrachelys gigantea*) en cautiverio y en estado silvestre, enfocándonos en: 1) la relación entre la temperatura ambiental y los patrones de actividad de las tortugas (n = 8 individuos silvestres), y 2) en las fluctuaciones de la temperatura corporal en las tortugas, incluyendo cómo su temperatura corporal interna y externa varían en relación a diferentes rangos de temperatura ambiental (estacionalidad; n = 4 individuos silvestre, y n = 5 individuos en cautiverio). En adición, examinamos la literatura para revisar el efecto de la masa corporal en el rango de temperatura corporal del grupo Testudinidae, con relación a temperaturas ambientales. La actividad diurna de las tortugas estuvo bimodalmente distribuida, y fue influenciada por la temperatura ambiental y la estacionalidad. La temperatura promedio en que la actividad fue maximizada fue de 27.9˚C, con un rango de 25.8–31.7˚C. Además, la temperatura del aire explicó los cambios en la temperatura interna corporal mejor que la masa corporal, y sólo durante el ensayo más frío las tortugas con mayor masa corporal exhibieron temperaturas más estables. Nuestros resultados, junto con la visión en conjunto del grupo Testudinidae, sugiere que, una vez la variación en la temperatura ambiental se ha tomado en cuenta, la masa corporal tiene un efecto mínimo en la estabilidad de la temperatura corporal interna de las tortugas. Por otra parte, la presencia de inercia térmica en cada individuo depende de la temperatura ambiental, y no encontramos evidencia de homeotermalidad inercial (‘inertial homeothermy’). Finalmente, los patrones de temperatura corporal interna y externa en comparación con las temperaturas ambientales sugiere que las tortugas gigantes de Aldabra actúan como conformadores-reguladores mixtos. Nuestro estudio provee una base para el manejo del ambiente térmico de poblaciones silvestres e introducidas de un importante ingeniero de ecosistemas en una era de cambio climático.

Introduction

Activity and body temperature of reptiles depend on the external thermal fluctuations in the environment and are both drivers and consequences of their physiological and behavioural biology, which ultimately affects their ecology (Heatwole 1976; Huey & Stevenson 1979; van Damme et al. 1991; Lailvaux & Irschick 2007). Many physical processes can affect the thermal environment of reptiles, including e.g., fluxes of radiative heat, convection, conduction, and wind (Cossins & Bowler 1987; Willmer et al. 2005). However, understanding this complex thermal environment alone does not allow an adequate description of a reptiles' activity patterns and core body temperature (T_{bc}; Table 1 lists the terms adopted here and their definitions). Rather than being thermally passive, i.e., with a body temperature driven only by fluctuations in environmental temperature, many reptiles have been shown to exhibit complex thermoregulatory behaviours and physiological processes to maintain their T_{bc} within a narrow range, albeit within limits determined by environmental conditions (Slip & Shine 1988; Paladino et al. 1990; Seebacher & Franklin 2001).

For example, when basking in sunny places, the common Puerto Rican ameiva (*Ameiva exsul*) can attain a T_{bc} that is higher than the air temperature (T_{air}), which allows them to be active later while foraging in the shade (Rivera-Vélez & Lewis 1994). In addition, salt water crocodiles (*Crocodylus porosus*) can employ shuttling behaviour between water and land to regulate their T_{bc} (Seebacher et al. 1999). On the other hand, eastern bearded dragons (*Amphibolurus barbatus*) can exert physiological reactions of metabolism and circulation in response to varying T_a to control heating and cooling rates and maintain preferred T_{bc} (Bartholomew & Tucker 1963). Furthermore, green iguanas (*Iguana iguana*) can display physiologically generated circadian rhythms in a constant environmental temperature, similar to those recorded in endotherms (Tosini & Menaker 1995).

Another factor considered important in influencing fluctuations of T_{bc} in reptiles is their body size, as the surface-to-volume ratio influences the rate at which heat is exchanged with the environment. Hence, due to a relatively small surface-to-volume ratio for larger reptiles, their T_{bc} is expected to be less responsive to the thermal environment than that of smaller ones (i.e., more stable; Zimmerman &

Tracy 1989). Body size also affects the rate of heat absorption from the sun (Brattstrom 1965), as larger bodies have a higher surface area, which in part drives their external body temperature (T_{be}). McNab and Auffenberg (1976) suggested that larger reptiles have a relatively low thermal conductance because their small surface-to-volume ratio and thick integuments could give them a substantial heat storage capacity, and because larger reptiles take longer to attain thermal equilibrium with the environment. For example, larger salt water crocodiles are able to attain not only higher, but also more stable T_{bc} than smaller ones, at least in part due to thermal inertia (Seebacher et al. 1999).

Here, we describe activity and body temperature fluctuations of Aldabra giant tortoises (*Aldabrachelys gigantea* Schweigger 1812) in both their natural habitat and in captivity. Specifically, we focus on: 1) the relationship between environmental temperature (T_a) and activity patterns of wild tortoises to determine their optimal environmental temperature range ($T_{a\text{-}opt}$); and 2) the body temperature fluctuations of captive and wild tortoises, including how their core and external body temperatures vary in relation to environmental temperatures, and whether body mass influences the response of tortoise core body temperatures to environmental temperatures. In addition, we surveyed the literature to investigate the effect of body mass on the body temperature ranges of Testudinidae in relation to air temperature.

Materials and methods

Study species and study sites

The Aldabra giant tortoise is endemic to Aldabra Atoll, Seychelles, with a stable population of an estimated 100,000 tortoises (Bourn et al. 1999; Turnbull et al. 2015). We studied wild tortoises on Picard Island, Aldabra, as well as captive ones in the Masoala Rainforest exhibit at Zürich Zoo, Switzerland. Aldabra is a raised coral atoll in the Western Indian Ocean, and has a tropical climate with a wet season (November to April) and a dry season (May to October). The timing and distribution of rainfall varies greatly from year to year, is unevenly distributed across the atoll, and directly drives spatio-temporal patterns in vegetation productivity (Shekeine et al. 2015; Haverkamp et al. 2017). In Zürich Zoo, the Masoala Rainforest exhibit is an

11,000 m^2 greenhouse ecosystem covered with translucent foil permitting 75% of daylight and 50% of UV radiation to enter, has an artificial rain- and fog systems, and an air-circulating heating system with the aims of maintaining minimum temperatures of 24˚ during the day and 18˚C during the night (Bauert et al. 2007).

Environmental temperatures and tortoise activity patterns

The environmental temperature range at which activities such as locomotion, feeding and mating occur in tortoises is narrow (Meek 1984). As other reptiles, tortoises have to select environmental temperatures that allow them to maintain T_{bc}s at which manifold processes are optimised to increase their fitness, e.g., physiological, locomotory and foraging ones. We examined activity patterns of wild tortoises in relation to air temperature (T_{air}) to derive an approximation for the optimal environmental temperature at which activity is maximised ($T_{a\text{-}opt}$). We derived activity based on accelerometer (ACC) data obtained from data loggers mounted on eight tortoises (06:00–24:00) for two years, as part of an ongoing long-term movement ecology study (we assumed no activity between 00:00–06:00). ACC data were recorded every five minutes for a burst of five seconds, during which 36 voltage readings were recorded. To assign a state of either active (1) or inactive (0) for/within each 5-min period, a rolling mean of the standard error (SE) of the ACC bursts was used to capture fluctuations in the ACC waveform. We set the threshold of the rolling average SE to five, to create binary data (similar to Nielsen et al. 2010). The activity data was then coupled with T_{air} obtained from the weather station located at the research station on Picard, which was collected every 15 min.

Body temperature of Aldabrachelys gigantea

We studied body temperature fluctuations in five captive tortoises from Zürich Zoo, and four wild tortoises from Aldabra. The zoo tortoises were housed in a compartment within the Masoala Rainforest exhibit, while the wild tortoises, selected for their different body masses (Table 2), were temporarily housed in two 36 m^2 enclosures located on Picard. Data from the captive tortoises were obtained

Table 1. Terms related to thermoregulation ecology used in this article.

Term	Definition
T_a	Available environmental temperature envelope (e.g., available T_{air} & T_{sun} in our case) for temperature regulation (e.g., throughout a given time period or study; ˚C).
$T_{a\ mean}$	Mean environmental temperature (from T_{air} & T_{sun}; ˚C).
T_{air}	Temperature recorded by loggers placed in a shaded area used by tortoises (equivalent to air temperature); and air temperature reported in studies for the review section; ˚C.
ΔT_{air}	Environmental temperature range given by the minimum and maximum temperatures recorded over a certain period from loggers placed in the shade (range in ˚C).
$T_{a\text{-}opt}$	Optimum mean air temperature at which activity is maximised (˚C).
$T_{a\text{-}opt\ range}$	Optimum air temperature range given by the minimum and maximum temperatures at which the active state surpasses the inactive state of tortoises (˚C).
T_{bc}	Core body temperature (i.e., gut temperature; ˚C).
ΔT_{bc}	Core body temperature range given by the minimum and maximum temperatures recorded over a certain period (˚C).
T_{be}	External (contact) body temperature (i.e., carapace, extremities and skinfold; ˚C).
T_{sun}	Temperature recorded by loggers placed in a sun-exposed area used by tortoises (includes radiative temperature; ˚C).

Definitions based and modified from (Cossins and Bowler, 1987; Blatteis *et al.* 2001; Willmer, Stone and Johnston, 2005).

during summer 2009 (ZRH summer; n = 3) and winter 2010 (ZRH winter; n = 5), while data from the wild tortoises were obtained during April 2014 (Aldabra; n = 4). In the course of the trials, all animals had *ad libitum* access to drinking water, food, and access to both shade and sunlight. Food consisted of hay, freshly cut grass and vegetables for the captive tortoises, and freshly cut leaves from native woody vegetation of known food species for the wild tortoises.

Environmental temperatures were recorded with temperature loggers every 15 min for all study periods. In Zürich Zoo, we used 11-bit Thermocron HC temperature loggers (±0.06˚C accuracy; OnSolution Pty Ltd., NSW, Australia), while

on Aldabra we used iButton® temperature loggers (±0.05˚C accuracy; Maxim Integrated, San Jose, CA, USA). In both sites, loggers were placed at two locations (shaded, and directly exposed to sunlight) at a height of 0.3–0.5m. Surface (external) body temperatures (T_{be}) were measured using infrared temperature pistols: *Raytek Fluke 566* in Zürich Zoo (0.01˚C accuracy; Raytek Corporation, Santa Cruz, USA), and *testo 810* on Aldabra (0.1˚C accuracy; Testo SA & Co., Mönchaltorf, Switzerland). To test whether logger and pistol data could be reliably compared, logger temperatures were directly measured using the infrared temperature pistol in Zürich Zoo, and data were highly correlated (T_{air}: $z = 150.68$, $p < 0.001$, Kendall $\tau = 0.89$; T_{sun}: $z = 84.05$, $p < 0.001$, Kendall $\tau = 0.89$). We fed temperature loggers to the tortoises and recorded their internal temperature (T_{bc}) every 15 minutes. Faeces were examined daily for the loggers, which were voided 10–20 days after ingestion. In Zürich Zoo, three tortoises (100–180 kg; see Table 2 for individual body masses) were fed the data loggers during the summer trial, and five tortoises for the winter trial (14–180 kg; same three individuals as in summer, plus two additional ones). On Aldabra, four tortoises (39–97 kg) were monitored. We additionally measured the following temperatures at 1–3 h intervals for a 48–72 h period, commencing five days after feeding the loggers to the tortoises: 1) surface of the carapace (the centre of each of the 13 main scutes, vertebral and costal), 2) the four extremities (each extremity in the region of the metacarpal/metatarsal joints), and 3) the deep skin folds (the skin at the deepest point underneath the carapace between each fore extremity and the neck, and next to each hind extremity; i.e., four measurements).

Body size and temperature in Testudinidae

To investigate thermal inertia, and inertial homeothermy, we collated data on ΔT_{bc}, ΔT_{air}, and on body mass in Testudinidae from the scientific literature. We searched the literature and selected studies that presented the aforementioned data for at least one Testudinid species, or summarised mean values for a group of individuals. When studies only showed results graphically, we extracted the data from figures using WebPlotDigitizer v. 3.10 (Rohatgi 2017, http://arohatgi.info/WebPlotDigitizer). We then assessed whether ΔT_{air} and/or *mass* significantly influenced ΔT_{bc} by using correlation analyses. We restricted our assessment to Testudinidae, rather than

Testudines, as oceanic/aquatic and semi-aquatic species are subject to different physical processes than terrestrial species (i.e., dissimilarities in heat dissipation caused by differences in convection and conduction properties of air and water).

Statistical analyses

We performed all statistical analyses using R v. 3.3.0 (R Core Team 2017), and report mean values and standard deviations (±SD). When plotting data, we fitted non-parametric locally weighted regressions using the nearest neighbour approach (loess; with t-based approximation 95% CI), using the package 'ggplot2' (Wickham 2016). We determined the temperature range at which tortoises maximise their activity ($T_{a\text{-}opt}$) by performing kernel density estimation. We partitioned the activity data in active and inactive states at a given temperature, which yielded a relative density distribution for each state with the area under the curve of the probability distributions adding to one. We visualised the kernel density estimation by partitioning the active and inactive states using R package 'ggplot2', and expected the distribution of the activity probability in response to environmental temperature to show a bimodal distribution for the inactive state, with the active state exhibiting greater levels of activity in between. In addition to calculating the T_{bc} ranges of the Aldabra giant tortoises and that of T_{air} and T_{sun}, we also fitted cosines of the angles to the observed T_{bc} data with circular-linear regression (e.g., Jammalamadaka & Lund 2006; Kinahan et al. 2007) using the R package 'psych' (Revelle 2016), and calculated the acrophase (time period during which the peak of T_{bc} occurs).

We used the package 'lme4' (Bates et al. 2015) to construct generalised linear mixed effects models with random factors (GLMMs) following Zuur et al. (2009). For the activity data, we tested the effects of *year*, *time*, *season* (wet and dry), T_{air}, and the interactions between *time* & *season*, and T_{air} & *season* on tortoise *activity* (active or inactive state; using logistic regression analysis with binomial family and link "log"; from here on "activity model"). We added *individual* (tortoise) and *day* (date) as random factors to account for individual variation and repeated

Table 2: Summary statistics of the environmental (T_{air} & T_{sun}) and core body temperatures (T_{bc}) of Aldabra giant tortoises (*Aldabrabrachelys gigantea*), with different body mass exposed to different thermal environments. Temperatures are indicated in degrees Celsius, and the acrophase is indicated in hours. The mean, maximum and minimum temperatures refers to the overall temperatures during the trials, while the range refers to the mean daily temperature range.

Environmental temperatures (T_{air} & T_{sun})

Environmental temperature	Study	Mean	±SD	Min	Max	Daily Range	Acrophase
Sun	ZRH Winter	18.0	3.0	14.4	32.1	10.3	14.0
Air (shade)	ZRH Winter	16.5	2.1	13.9	23.7	6.4	14.9
Mean	ZRH Winter	17.2	2.5	14.2	27.4	8.2	14.4
Sun	ZRH Summer	25.4	5.4	18.2	36.6	15.3	14.5
Air (shade)	ZRH Summer	22.0	3.1	17.1	28.6	8.7	15.3
Mean	ZRH Summer	23.7	4.2	17.7	32.6	11.8	14.7
Sun	Aldabra	31.6	7.3	23.0	56.5	18.5	14.0
Air (shade)	Aldabra	29.1	2.5	24.0	38.5	6.5	15.9
Mean	Aldabra	30.3	4.4	23.8	43.8	12.4	14.5

Tortoise core body temperature (T_{bc})

Tortoise	Mass (kg)	Study	Mean	±SD	Min	Max	Daily Range	Acrophase
JVS	14	ZRH Winter	20.8	1.6	17.0	26.0	3.1	19.04
JVL	19	ZRH Winter	21.5	1.3	18.6	25.5	2.7	20.26
HMA	100	ZRH Winter	22.2	0.9	20.1	24.6	1.4	20.98
SBY	140	ZRH Winter	21.1	1.0	19.2	23.9	1.6	20.28
BBY	180	ZRH Winter	20.5	0.8	18.4	23.0	1.5	21.53
HMA	100	ZRH Summer	29.9	2.1	25.1	34.1	5.0	19.63
SBY	140	ZRH Summer	30.1	2.4	24.7	34.2	5.7	20.03
BBY	180	ZRH Summer	29.7	2.0	24.2	33.2	4.7	20.57
BEL	39	Aldabra	29.9	1.6	26.0	34.5	4.7	18.13
UNM	48	Aldabra	29.9	1.7	26.0	34.0	4.9	17.86
CFK	61	Aldabra	30.2	1.6	26.5	35.0	4.4	18.34
LDX	97	Aldabra	31.0	1.7	26.0	34.5	5.0	17.86

measures. The analysis was limited to 06:00–20:00, and the wet season comprised the months November–April and the dry season May–October. To account for the non-linear relationship between *activity* and *time*, we discretised continuous time into four periods (I– IV), following the overall activity turning points through time, and comprising 06:00–08:00, 08:15–13:30, 13:45–17:30 and 17:45–20:00, respectively (see Appendix 7). Furthermore, to assess the factors that influence T_{bc} of giant tortoises during our trials, we tested the following predictor variables: *trial*, *time*, T_{air}, *mass* and the interaction between T_{air} and *mass* (from here on

"thermoregulation model"). We included a random factor with individual tortoises interacting with *trial*, and a random factor with day (date) to account for individual variation and repeated measures amongst trials. Because they are correlated, T_{air} was selected over T_{sun} and $T_{a\ mean}$ as a predictor based on model selection (ΔAIC). Moreover, and similar to the activity model, we discretised continuous time into three periods (I–III) following the turning points of T_{bc} through time for each independent trial, and comprising the morning period when tortoises are cooling down, the morning-afternoon period when tortoises are heating up, and the night period when tortoises start to cool down, respectively, to account for the non-linear relationship between T_{bc} and *time* (see Appendix 8). We obtained *p*-values for the predictor variables by using the Satterthwaite degrees of freedom approximation (implemented in package 'lmerTest' for the thermoregulation model; Kuznetsova et al. 2016).

Results

Environmental temperature and tortoise activity patterns

Diurnal activity of Aldabra giant tortoises on Aldabra was bimodally distributed, with the highest activity levels occurring during the morning, and during the late afternoon, albeit at comparatively lower levels (Fig. 1). The mean T_{air} during the active state was 27.9˚C (±2.6; 25–75% quartile = 26.0–29.6˚C). Notably, the probability of activity rapidly decreased as the environmental temperature increased above ca. 31–32˚C (Fig. 2A). Moreover, the kernel frequency distribution of the active state highlights that the temperature range of the active state in tortoises is 25.8–31.7˚C (Fig. 2B). In the activity model, the activity patterns of tortoises were significantly influenced by T_{air}, as well as *time*, *season* and the interactions between T_{air} and *time*, and T_{air} and *season* ($p < 0.001$), but not by year ($p = 0.87$; see Appendix 9 for model statistics, and Appendix 10 for seasonality plot).

Body temperature of Aldabrachelys gigantea

Temperatures measured in shaded and sunny areas in each of the trials had similar daily minima but different maxima (Table 2), with considerable day-to-day variation in all trials (Fig. 3). On Aldabra, we recorded relatively higher temperatures,

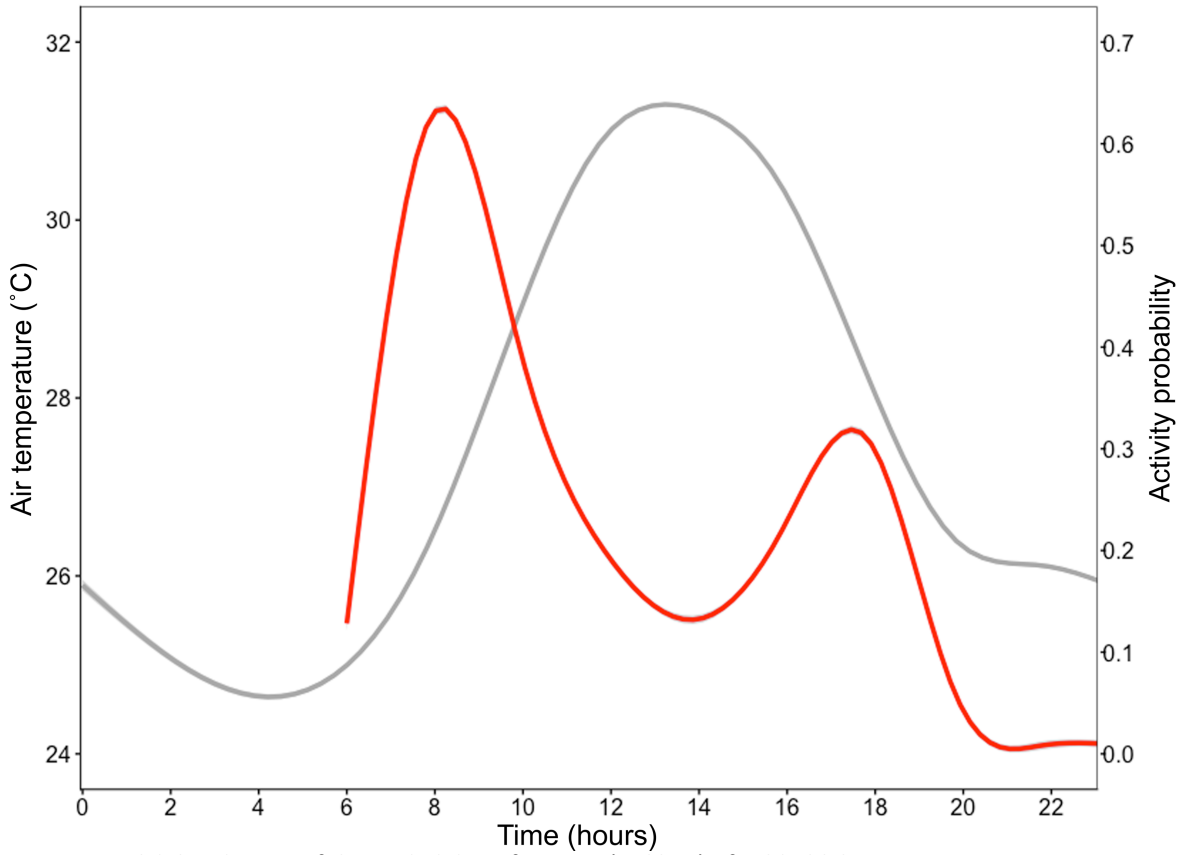

Figure 1: Bimodal distribution of the probability of activity (red line) of wild Aldabra giant tortoises (*Aldabrachelys gigantea*) and environmental temperature (grey line) per hour/day. Line smoothing by local regression loess.

in some cases above 40˚C, in the sunny areas. The general daily patterns of T_{bc} lagged behind those of T_a. Tortoises on Aldabra seemed to behave as thermoconformers at the beginning of the trial (first five days, where the T_{bc} of tortoises followed T_a closely). At the beginning of the ZRH summer trial, the 100 kg individual seems to have avoided basking in the sun. During the trials, there were some perturbations in the T_a cycles, and the ability of tortoises to cope with these depended on the direction of the perturbation. Tortoises were able to maintain a stable T_{bc} when T_a increased above normal levels (e.g., Aldabra), but had difficulties doing so when T_a decreased sharply (e.g., ZRH summer and the last day at Aldabra). Overall, tortoises were able to maintain their T_{bc} above low mean T_a, and below high mean T_a. Tortoises maintained their mean T_{bc} at 30.1˚C ±1.9 during the ZRH summer and Aldabra trials (for all tortoises combined, n = 7; Table 2). In contrast, during the ZRH winter trial, tortoises maintained a mean T_{bc} of 21.2°C ±1.3, albeit higher than

mean T_a. The mean daily T_{bc} of tortoises varied by 3.7˚C ±0.9 on Aldabra, 4.7˚C ±1.2 during ZRH summer, and 4.9˚C ±1.0 during ZRH winter. Moreover, only during the winter trial, where juveniles were included, did we observe that the rate of heat loss during the night increased as mass decreased (Fig. 3). On the other hand, only on Aldabra when T_a was above 25˚C did the T_{bc} of tortoises reach values very close to the minimum T_a.

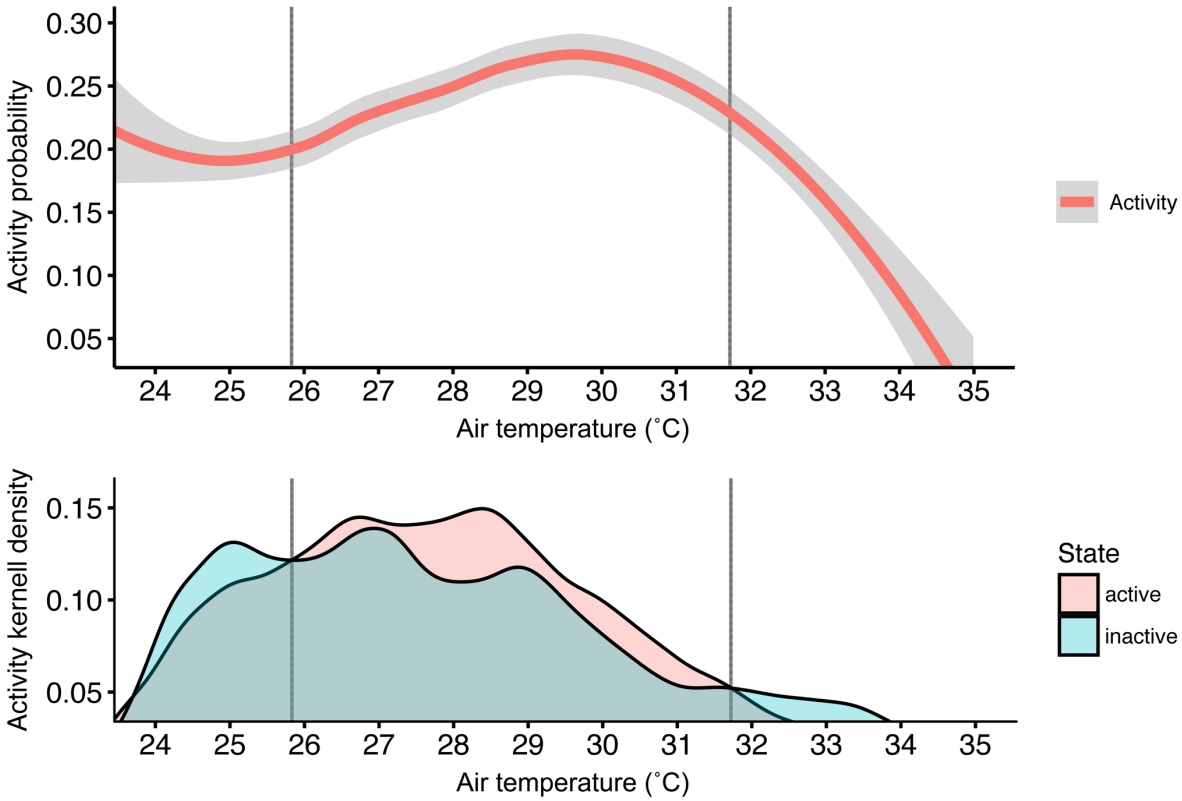

Figure 2: Probability of Aldabra giant tortoise (*Aldabrachelys gigantea*) activity as a response to air temperature (T_{air}) (a), and kernel density plot of active and inactive states for a given T_{air} (b). Line smoothing by local regression loess (shading indicates the 95% CI). Vertical lines delimit the temperature range at which activity is maximised. T_{air} was recorded from Picard Island weather station daily along with tortoise activity data from eight individuals during 2013–2014.

Viewing the aggregated variability of the tortoises' T_{bc} over a 24-hour period, the variable dependence of the effects of mass on T_a (due to different T_a ranges available), and their influence on T_{bc} became clear (Fig. 4). During winter, the magnitude of the response of T_{bc} to daily changes in T_a decreased with size, and only the smallest tortoises were able to briefly reach T_{bc} close to $T_{a\text{-}opt}$. However, as $T_{a\ mean}$ reached values and temperature ranges closer to $T_{a\text{-}opt}$, larger tortoises were able to increase and maintain their mean T_{bc} close to the upper range of $T_{a\text{-}opt}$ (i.e., ZRH

summer and Aldabra trials). In general, as $T_{a\ mean}$ and minimum T_a increased, so did the T_{bc} of the tortoises (Table 2), but most of T_{bc} readings remained above $T_{a\ mean}$.

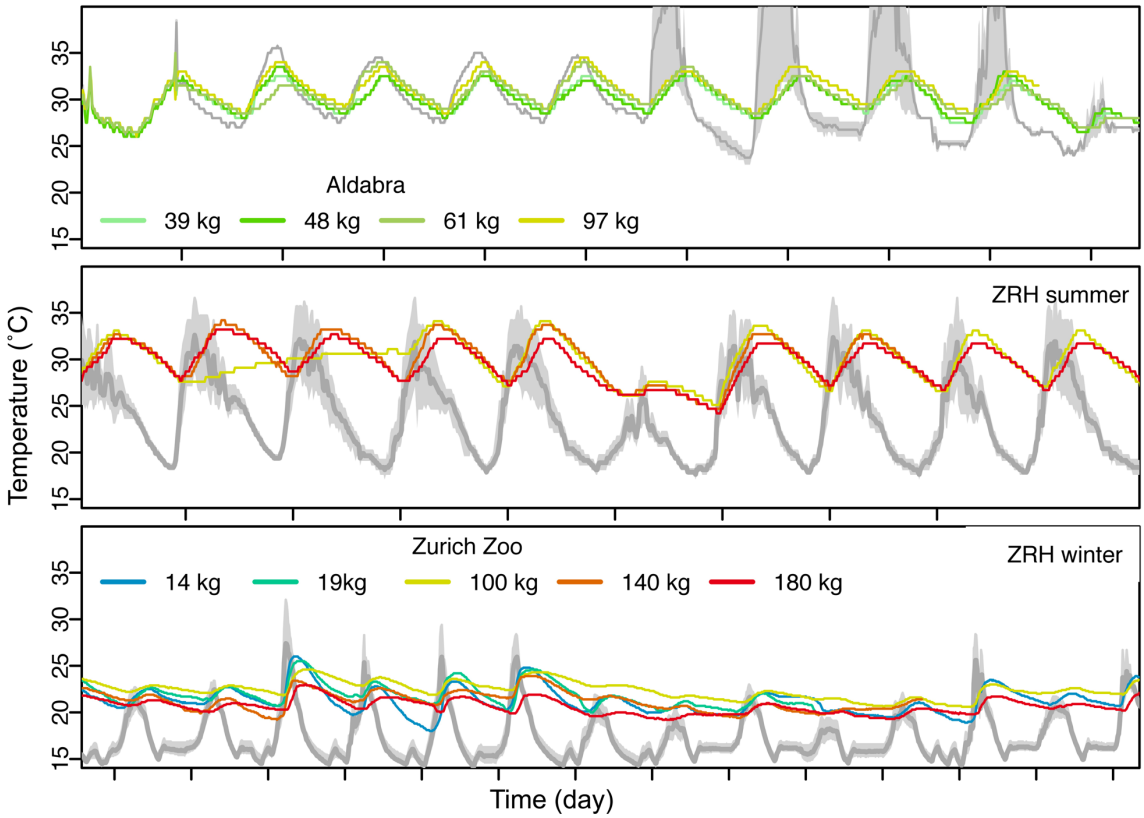

Figure 3. Temporal fluctuations in the environmental temperature range (T_{air} and T_{sun}; grey fill) and core temperature recorded by data loggers in the gastrointestinal tract of Aldabra giant tortoises (*Aldabrachelys gigantea*) in different trials. The dark grey line depicts $T_{a\ mean}$, and cool to warm coloured lines depict ascending mass range for individual tortoises (with mass given in the legend) One trial was performed on Aldabra Atoll with wild tortoises, and two trials were performed at Zürich Zoo (during winter and summer). Tick marks in the x-axis depict a 24h interval: peaks of environmental temperature indicate temperature at ~mid-day, and lowest point of the valleys indicate temperatures at ~midnight.

The magnitude of daily ΔT_{bc} differed among trials (Table 2). Overall, there was a positive correlation between the daily ΔT_{bc} and ΔT_{air}, but it was only significant for the ZRH trials (z = 5.87 and 4.12, $p < 0.01$, *Kendall* τ = 0.43 and 0.55 for the winter and summer trials, respectively). On Aldabra, there was no significant correlation (z = 1.46, p = 0.14, *Kendall* τ = 0.16). For ZRH winter, ΔT_{bc} decreased from the smallest to the largest animal (z = -4.76, $p < 0.001$, *Kendall* τ = -0.37). In contrast, ΔT_{bc} of tortoises during ZRH summer (without smaller, juvenile tortoises) and on Aldabra remained virtually the same between individuals of different mass (z = -0.73 and 0.28, p = 0.47 and p = 0.78, Kendall τ = -0.10 and 0.03, respectively). Moreover, in

ZRH winter, the $\Delta T_{bc}/\Delta T_{air}$ quotient was negatively correlated with tortoise body mass (z = -5.87, p < 0.001, *Kendall* τ = -0.45). However, we found no correlation in the ZRH summer trial (where no juveniles were included) or the Aldabra trial (z = -0.71 and 0.12, p = 0.48 and 0.91, Kendall τ = -0.10 and 0.01, respectively).

There was greater variation in T_{be} than in T_{bc} (Fig. 5; see Appendix 11 for summary statistics). Daily temperature fluctuations were greater on the carapace surface than on the surface of the extremities, which in turn were greater than in the skin folds or in the core body temperature. Temporal turning points of the temperature curves occurred first in the environment, followed by the carapace, the extremities, the skin folds and, finally, the core. Temperatures of the carapace and extremities were also correlated with T_{bc}, but to a lesser degree (z = 33.38, p < 0.001, Kendall τ = 0.70, and z = 51.28, p < 0.001, Kendall τ = 0.59, respectively), and remained lower than T_{bc} (Wilcoxon Rank Sum Test, p < 0.001 in both cases). The temperature recorded in the skin folds was highly correlated with, but remained lower than T_{bc} (z = 37.77, p < 0.001, Kendall τ = 0.79; Wilcoxon Rank Sum Test, p < 0.001).

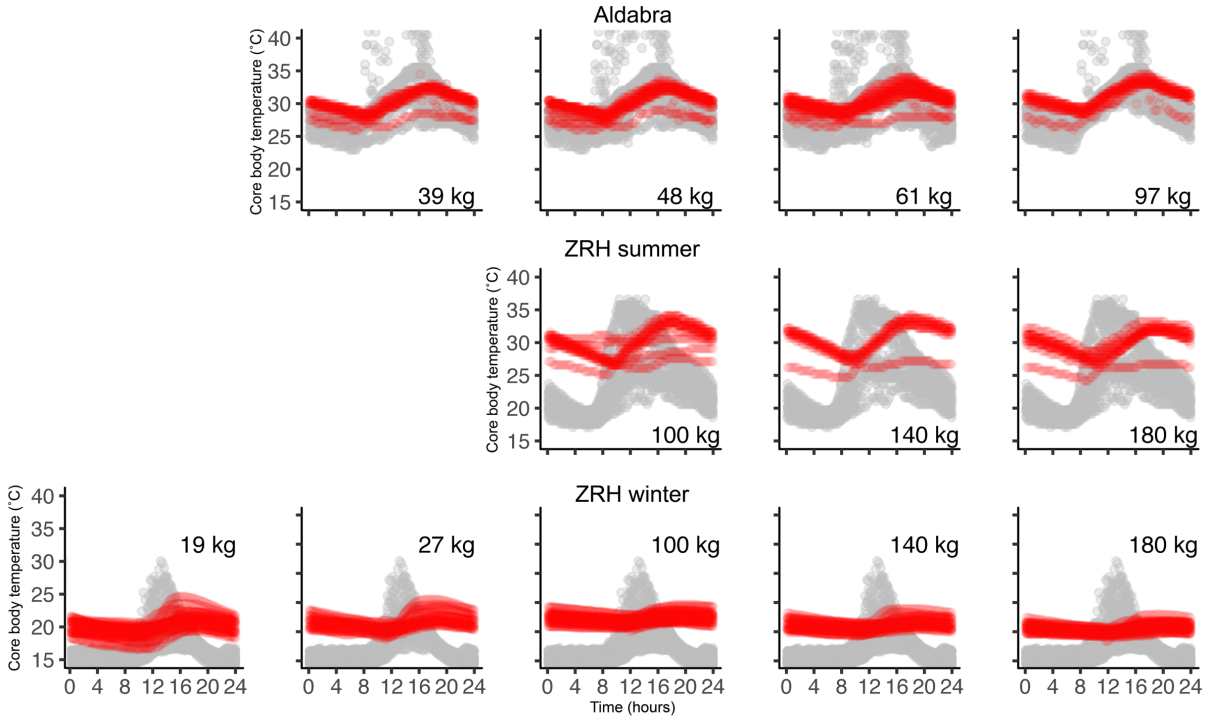

Figure 4: Daily environmental temperatures (grey; T_{air} & T_{sun}), and core body temperature (red; T_{bc}) of Aldabra giant tortoises (*Aldabrachelys gigantea*) of different mass across different environmental temperature ranges (trials).

All explanatory variables of the thermoregulation model, *trial*, *time*, T_{air}, *mass* and the interaction between T_{air} and *mass*, influenced the variation in T_{bc} at $p < 0.001$ (see Appendix 12 for model summary statistics). When considered independently, T_{air} better explained the variation of the T_{bc} of tortoises than mass (ΔAIC = 1668), or the interaction between T_{air} and mass (ΔAIC = 1128). The relationship between mass and T_{bc} in ZRH winter is bell-shaped, increasing until it reaches 100 kg and then decreasing again. In contrast, T_{bc} did not exhibit any clear pattern in relation to mass in the summer trial (where no juveniles were used and hence the body mass range was much smaller than during winter), while on Aldabra T_{bc} showed a slight increase with mass (Table 2). Similar patterns to those exhibited by the relationship between mass and T_{bc} for each trial were observed for the acrophase, and the time lag of T_{bc} to acrophase (i.e., the time difference at which T_{bc} reaches the acrophase in relation to T_a).

For the relationship between T_a and T_{bc} for all tortoises in our study, most of the data points lay above T_a and slowly shifted towards lower values after T_a reached >30˚C (Fig. 6). As before, the variation in T_{bc} decreased with increasing size only during the winter trial. Interestingly, the T_{bc} trend increased more sharply with increasing T_{air} (temperature of shaded areas where they seek refuge) in contrast to T_{sun}.

Body size and temperature in Testudinidae

In addition to our data, we were able to gather 22 measurements of six species in four genera, from six studies (Benedict 1932; Mackay 1964; Swingland & Frazier 1979; Meek & Jayes 1982; Huot-Daubremont et al. 1996; McMaster & Downs 2013c). Seven of these 22 data points contain estimated mass values from various individuals, and methods for measuring temperature varied (see Appendix 13 for details).

The ΔT_{bc} of different Testudinid species was negatively correlated with their mass (z = -3.11, p = 0.002, *Kendall* τ -0.38; Fig. 7A). However, the ΔT_{bc} of tortoises was more strongly positively correlated with ΔT_{air} (z = 4.60, $p < 0.001$, Kendall τ = 0.57; Fig. 7B). When corrected for ΔT_{air} (using the ratio of the of ΔT_{bc} to ΔT_{air}), there

was a weaker negative correlation between $\Delta T_{bc}/\Delta T_{air}$ the and *mass* (z = -2.42, p = 0.02, *Kendall* τ –0.29; Fig. 7C).

Discussion

Abiotic, biotic, physiological and behavioural factors play an important role in the regulation of body temperature of reptiles. Here we described the activity patterns of Aldabra giant tortoises in relation to the environmental temperature, the optimum environmental temperature at which tortoises maximise their activity, and how different gradients of environmental temperatures and body mass influenced the variation in their internal and external body temperatures. Moreover, we found evidence of thermal inertia, but this effect seemed to be context dependent in terms of the environmental temperatures experienced by the tortoises, and the overall Testudinidae dataset indicated little effect of mass on the temperature stability of tortoises.

Environmental temperature and tortoise activity patterns

We used activity patterns of Aldabra tortoises in response to T_{air} to identify the temperature range at which activity is maximised, and use this as a proxy for optimal environmental temperature range, $T_{a\text{-}opt}$. The activity of Aldabra giant tortoises is similar to that of other tortoise species, including southern Africa's largest tortoise, the leopard tortoise (*Stigmochelys pardalis*; Monadjem et al. 2013; McMaster & Downs 2013a; 2013c). Similar to Aldabra giant tortoises (RPB et al. unpubl. data.), leopard tortoises exhibit a transition in daily activity patterns across seasons, being unimodal during the dry-cold season, and shifting progressively towards bimodal as the season transitions towards hot and wet. In addition, under similar T_a conditions as those experienced by Aldabra giant tortoises (i.e., during the Nama-Karoo South African summer), leopard tortoises started becoming inactive when T_a increased above 30.5–32˚C between 10:00–11:00h (McMaster & Downs 2013a), when presumably tortoises seek shade to cool down. Moreover, Lambert (1981) found similar relationships between temperature and activity in the spur-thighed tortoise (*Testudo graeca*), although these tortoises were active at a lower temperature range of 18–28˚C and inactive when T_a was below 18˚C. The T_a threshold for switching

from a unimodal to bimodal activity pattern in *T. graeca* was 28˚C. Aldabra giant tortoises maximise their activity ($T_{a\text{-}opt}$) in the temperature range of 25.8–31.7˚C. This is within the preferred temperature range (i.e., the range of T_{bc} within which an ectotherm seeks to maintain itself by behavioural means) of other Testudinid species, with reported ranges of 25–31˚C (*Gopherus agassizii*; Woodbury & Hardy 1948; *G. agassizii* and *Testudo hermanni*, Brattstrom 1965; *T. marginata* and *T. hermanni*, Panagiota & Valakos 1992; Huot-Daubremont et al. 1996).

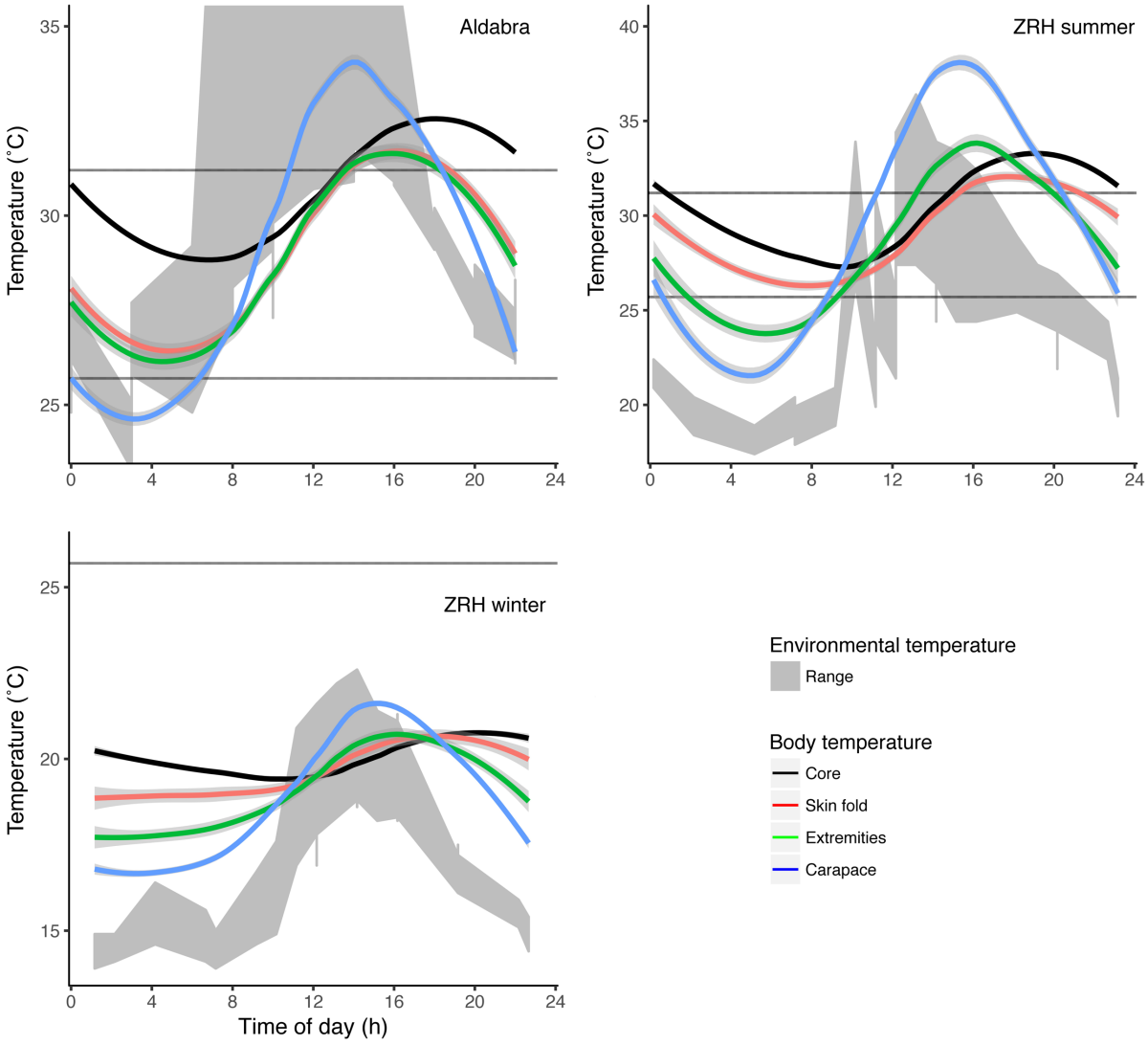

Figure 5: Average daily fluctuations of environmental temperature and Aldabra giant tortoise (*Aldabrachelys gigantea*) body temperatures on Aldabra Atoll and the Zürich Zoo (winter and summer). Note that the y-axis is scaled independently for each trial. The range intervals of T_a (maxima & minima) are depicted in grey shading in the background. The shading around the lines represents the 95% CI based on the line smoothing by local regression–loess. For the Aldabra trial, sun temperatures go beyond the y-axis limits.

Moreover, the range of mean T_{bc} maintained by wild Galápagos (*Chelonoidis nigra*) and Aldabra giant tortoises was within $T_{a\text{-}opt}$ (Mackay 1964; Swingland & Frazier 1979; this study). Rather than preferred body temperatures, we calculated $T_{a\text{-}opt}$, and our environmental temperature measurements were done in the shade. Because tortoises may be exposed to the sun when active, our measured optimal environmental temperature range may be biased to the lower limits of $T_{a\text{-}opt}$ (i.e., $T_{a\text{-}opt}$ may actually be higher). However, the pronounced drop in activity probability once temperature in the shade (T_{air}) increases above 31˚C (upper limit of $T_{a\text{-}opt\ range}$), as well as the clear thermoregulatory pattern exhibited by tortoises when T_{bc} reaches this temperature, suggest that the upper limit of the preferred core body temperature range is around 31˚C. This is in accordance with the findings of Swingland & Frazier (1979), who reported the maximum critical temperature for Aldabra giant tortoises in the wild to be 36–38˚C (measured in tortoises dying or that recently died from overheating in the wild). Therefore, the $T_{a\text{-}opt\ range}$ in combination with the mean T_{bc} of wild tortoises may serve as a reference for a high quality thermal environment for husbandry and captive care practices (e.g., McArthur & Barrows 2008) and conservation efforts with regards to climate change and thermal refuge availability (e.g., Swingland & Frazier 1979; Moulherat et al. 2014).

Although the activity of tortoises was affected by seasonality, our results are likely to capture the full extent of environmental temperatures at which Aldabra tortoises maximise their activity because we include activity and temperature data from a two-year period. However, the data show the flexibility of tortoises with regards to their activity patterns and available T_{air}, depicted by the variation of the seasonal activity patterns in relation to temperature. Other tortoises also show flexibility in terms of their activity in relation to seasonal changes in temperature (amongst other factors, see McMaster & Downs 2013a). Rainfall and temperature have been shown to be important factors influencing the activity of tortoises (Kazmaier et al. 2011). In our activity model, the interaction between the dry season and T_{air} negatively affected activity. We thus hypothesise that the changes in activity patterns dependent on seasons in Aldabra giant tortoises may also be driven by changes in water balance and water conservation. Water balance is important in tortoises because it affects their food consumption, diet, daily behaviour,

osmoregulation and body mass (Nagy & Medica 1986). Tortoises have been shown to suffer significant evaporative water loss from their integuments and through respiration (Schmidt-Nielse & Bentley 1966). Moreover, increasing temperatures and drought conditions have been shown to increase water loss through evaporation in tortoises (Cloudsley-Thompson 1968; Minnich 1977). The expected main mechanism for thermoregulation in tortoises is to change their daily activity levels and behaviour (because the rigid shell limits the effectiveness of postural changes during behavioural thermoregulation; McMaster & Downs 2013c). To conserve water, tortoises may decrease their activity levels and stay in the shade during and after the warmest part of the day in the dry season. If our hypothesis is correct, we can expect that the increasing frequency of drought periods on Aldabra (Haverkamp et al. 2017) will have negative impacts on the activity of giant tortoises.

It should be noted that temperature is not the only factor influencing the activity of tortoises. For example, Gibson & Hamilton (1983) hypothesised that seasonal changes in the activity of Aldabra giant tortoises were in response to food availability. Moreover, precipitation, solar radiation and wind velocity also seem to play a role in determining the bimodal to unimodal activity patterns and the activity levels of Aldabra giant tortoises (unpubl. data). Further research is being undertaken to determine the environmental drivers of the activity of Aldabra giant tortoises on Aldabra.

Body temperature of Aldabrachelys gigantea

Fluctuations in T_{bc} lagged behind those of T_a, and in general tortoises heated more rapidly during the day than they lost heat during the night, when T_{bc} fell slowly. During the ZRH winter trial, T_{bc} was always higher than T_{air}; only the temperature logger placed in direct sunlight recorded temperatures that were higher than T_{bc}, especially during the middle of the day. T_{air} better explained T_{bc} of tortoises, and in general, they were able to maintain their T_{bc} above low T_{air}, and below high T_{air}, and their T_{bc} was affected by the range of available environmental temperatures. Moreover, the temperatures measured on the surface of the carapaces were notably higher than T_{air} during the morning, which is evidence for thermoregulation via basking behaviour (e.g., Lambert 1981; Crawford et al. 1983). While basking, reptiles

reach higher core temperatures than air temperatures, and T_{bc} correlates positively with time spent basking (Boyer 1965; Rivera-Vélez & Lewis 1994). Correspondingly, T_{bc} dropped in cloudy days, when basking was not possible, and environmental temperatures dropped by 3–5˚C. During ZRH summer and on Aldabra, the mean and the range of T_a was higher, and tortoises were able to maintain their T_{bc} close to $T_{a\text{-}opt}$. On Aldabra, we recorded some extreme high temperatures in the sun during the second half of the study, probably due to clear skies and virtually no wind, but tortoises were able to maintain a stable T_{bc} nonetheless. Swingland and Frazier (1979) reported very similar patterns of T_{bc} for *A. gigantea* to those exhibited by our tortoises, but in the southeast of the atoll on Grande Terre island, where shade is more limited and where the size dimorphism of tortoises is much less pronounced. Additionally, Mackay (1964) observed similar patterns of T_{bc} in two Galápagos giant tortoises (65 and 170 kg), which were able to maintain their T_{bc} within ~28–32˚C when the mean T_a was ca. 28˚C and fluctuated between ca. 23–35˚C, despite the difference in their mass.

As found in leopard tortoises (McMaster & Downs 2013b), the differential variation in T_{be} of different body surfaces and as well as that of T_{bc}, indicated that there are large thermal gradients within the bodies of Aldabra giant tortoises. For example, the maximum carapace temperature of Aldabra giant tortoises in our study sometimes greatly exceeded that of their recorded T_{bc}, to the point that it surpassed the maximum critical temperature (of T_{bc}) recorded for the species. Studying the thermoregulation of Galápagos giant tortoises, Mackay (1964) proposed, based on the temperature differential between the core body temperature and the carapace, that heat flows through a limited region with high resistance when compared to that of the material absorbing the heat. We found the same pattern in Aldabra giant tortoises, where the integral of the difference between the T_{bc} and the carapace temperature (mean of the vertebral and costal scutes) followed the same temporal pattern as that of T_{bc}. While in the shade, the temperature of the scutes on the carapace of the tortoises remained above shaded environmental temperatures as well as above the T_{bc}, indicating that they lost heat to the environment. In contrast,

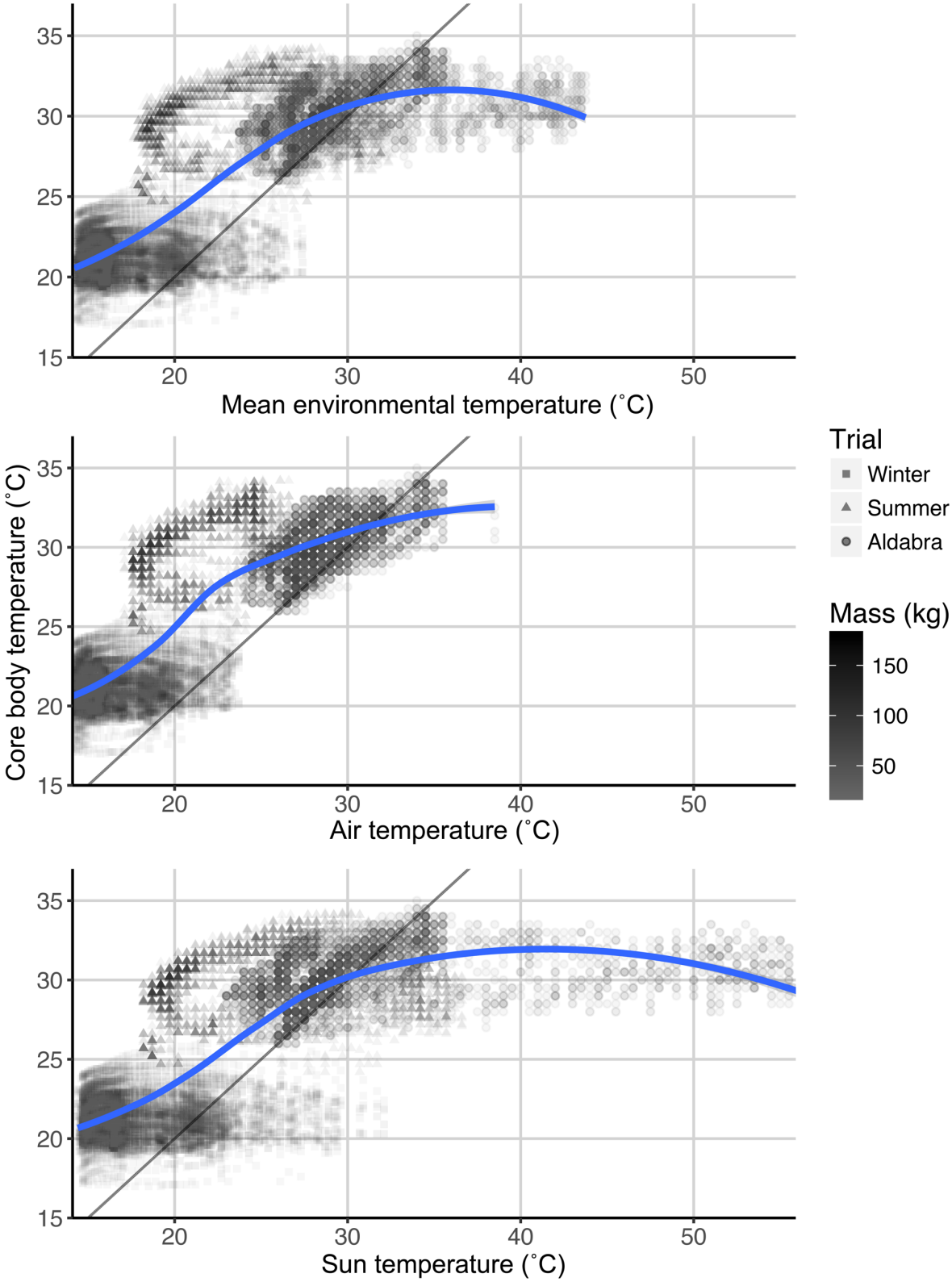

Figure 6: Aldabra giant tortoise (*Aldabrachelys gigantea*) core body temperature (T_{bc}) in relation to mean environmental temperatures ($T_{a\ mean}$; a), air temperature (T_{air}, in the shade; b), and in the sun-exposed areas (T_{sun}; c). Points represent the T_{bc} of tortoises, with the grey-colour gradient indicating body mass, and trials indicated by shape. The line represents a 1:1 response, while the blue lines represent the response of the tortoises' T_{bc} (all animals per trial combined) to environmental temperatures based on smoothing by local regression–loess (the shading represents the 95% CI).

at night, carapace temperatures dropped below T_{bc}, and were closer to T_a than that of the extremities or skin folds (which were also below T_{bc}). Thus, our results suggest that Aldabra giant tortoises employ different behavioural and physiological mechanisms to use their carapace as a heat exchanger: a heat collector in the mornings, a radiator (i.e., cooling system) during the warmest part of the day, and an insulator during the coldest part (see McMaster & Downs 2013b, and references therein, for a discussion of the differential temperature of T_{bc} and T_{be} in tortoises and possible control mechanisms).

It is worth noting that Aldabra hosted a population of introduced goats until 2012, when an eradication programme was completed (Bunbury et al. 2013). In 1985, during the same time as the tortoise population decline from an estimated 130,000 to around 100,000 (Bourn et al. 1999), Coblentz and Vuren (1987) estimated that there were as many as 1,300 goats on Aldabra. They suggested that the major impact of the goats was their negative effect on shade resources through over-browsing, rather than direct competition with tortoises for food. Our results suggest a strong role of available shade for structuring tortoise activity and in body temperature regulation, supporting the likelihood of over-browsing by goats having had a negative impact on Aldabra's giant tortoises.

Body size and temperature in Testudinidae

Thermal inertia likely explains why after basking, tortoises at the Zürich Zoo had higher T_{bc} than minimum T_a during early mornings on the next day, and cooling rates appeared to decrease with size. However, the effect of mass on temperature stability of Aldabra giant tortoises (ΔT_{bc}) differed by trial. When the mean T_a was 17.2˚C during the ZRH winter trial, T_{bc} stability increased with increasing size. This was not the case for the mean T_{bc}. In ZRH winter, the tortoise of intermediate size (100 kg) had the highest mean T_{bc}, suggesting that both the fast cooling rate of small animals, and the slow heating rate of larger animals, influenced their mean T_{bc}. On the other hand, ΔT_{bc}, as well as the mean core body temperatures in ZRH summer and on Aldabra did not seem to vary with mass. Furthermore, there was a tendency for the acrophase of tortoises (time at which T_{bc} peaked), and of the thermal lag of T_{bc} to T_a, to increase with mass in the Zürich tortoises, but there was no apparent

trend on Aldabra. Also, the effect size of mass in our thermoregulation model was rather small, and T_{air} better explained changes in the T_{bc} of Aldabra giant tortoises. Moreover, the analysis on the overall Testudinidae dataset appears to indicate that within the body size range of the tortoise species studied, large individuals are subject to similar fluctuations in body temperature as smaller ones once variation in air temperature has been taken into account. Thus, the presence of thermal inertia in tortoises seems to depend on the environmental temperatures. However, it is notable that behavioural thermoregulation and acclimatisation can potentially override the effects of mass on the T_{bc} of tortoises, and thus provide an alternative, and possibly synergistic explanation of the apparent context-dependent effect of mass on T_{bc}.

In addition, the notion that large ectotherms may maintain a high (30˚C) and stable T_{bc} within a narrow range (2˚C) due to mass-dependent thermal inertia, similar to homeothermic endotherms, is often referred to as 'inertial homeothermy' (McNab & Auffenberg 1976; Seebacher 2003). Despite being 'giants', even under stable conditions, the range of T_{bc} in Aldabra giant tortoises (as well as other species of smaller tortoises) was much larger than 2˚C. These results indicate that that inertial homeothermy is not possible in tortoises with the range of body masses studied. These findings support the conclusion of Grigg et al. (2004), who found that inertial homeothermy over the course of a single day is only found in large ectotherms above 500 kg of body size.

Conclusions

Despite the large sizes that Aldabra giant tortoises can attain, and the presence of thermal inertia, our results suggest that tortoises are incapable of regulating their core body temperatures within a range narrow enough to be considered inertial homeotherms. Rather, the interplay between the mass of the tortoises and the variation of T_a, in combination with behavioural thermoregulation, limits the degree to which these ectotherms can attain core body temperatures close to their presumed optimum T_{bc}. We found evidence of thermoregulation, where tortoises

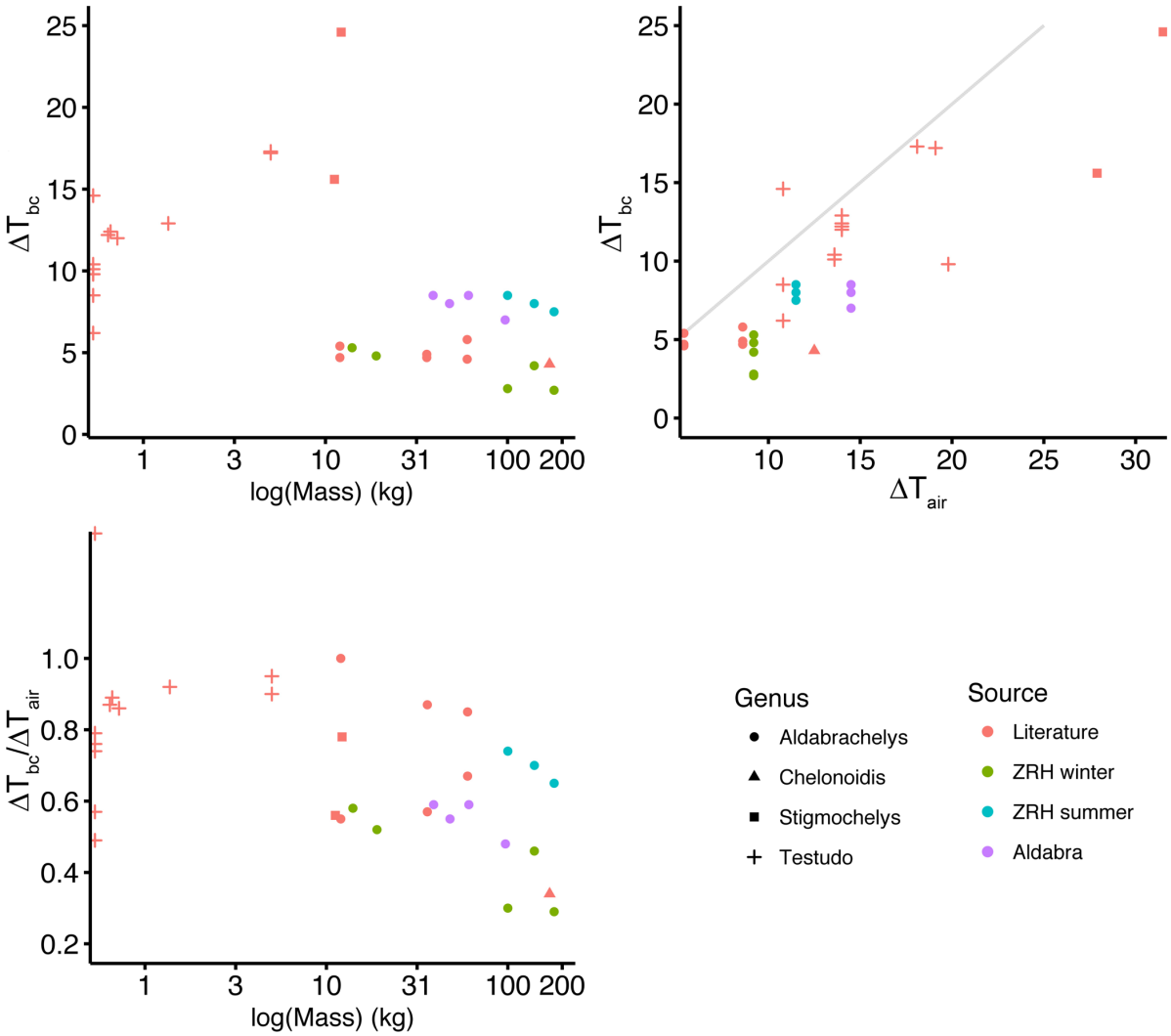

Figure 7: Core body temperature ranges (ΔT_{bc}) of Testudines in relation to the environmental temperature range (ΔT_{air}) and their mass. Relationship between ΔT_{bc} and mass (a), ΔT_{bc} and ΔT_{air} (b), and between the ΔT_{bc} to ΔT_{air} ratio (to control for environmental temperature; c). Point shapes indicate the genus, and colour indicates the source of the data. In panel c, one of the points is > 1, probably because the air temperature did not capture the environmental temperature at which the tortoise was exposed (e.g., if the tortoise was mainly basking in the sun).

were able to maintain T_{bc}s independent of T_a. We also found instances of thermoconformity, and when we evaluated T_{bc} in response to T_a, our results indicate that giant tortoises act as mixed conformer-regulators (Willmer et al. 2005). However, although the relationship between T_{bc} and T_a suggests that giant tortoises can maintain a stable T_{bc} when the mean T_a is above the lethal temperature (>36˚C), evaluating the components of T_a independently (the temperature of shade and sun exposed loggers) shows that Aldabra giant tortoises have a limit: when shade temperature (T_{air}) surpasses ca. 31˚C, the T_{bc} seems to keep increasing rather than

reaching a plateau. While some tortoises can adjust their behaviour to survive extreme environmental temperatures (e.g., *Gopherus agassizii* can remain active even when T_a reaches ca. 60˚C by adjusting the time spent in burrows; Zimmerman et al. 1994), larger animals such as *A. gigantea* have limited options. The plasticity and intra- and interspecific variation in tortoises, and other reptiles, certainly allows for the animals to respond to the selective pressures imposed by the environment. However, it is likely that climate change will accentuate thermoregulatory pressures (Barrows 2011; Gunderson & Stillman 2015), especially on larger species.

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5

EVALUATION OF ARTIFICIAL HEATING SOURCES FOR THE THERMOREGULATION OF ALDABRA GIANT TORTOISES IN ZÜRICH ZOO

CHAPTER 5

Evaluation of Artificial Heating Sources for the Thermoregulation of Aldabra Giant Tortoises (*Aldabrachelys gigantea*) in Zürich Zoo

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Abstract

We evaluated the effectiveness of the installation of a heating area (concrete heat pad and basking lamp) in aiding thermoregulation of Aldabra giant tortoises (*Aldabrachelys gigantea*) at Zürich Zoo, Switzerland. We recorded the thermoregulatory patterns of five tortoises (25–193 kg) during spring (ZRH spring trial), and compared this to published results on the same tortoises observed prior to the installation of the heater (ZRH summer and winter trials), and on wild tortoises on Aldabra Atoll. The mean environmental temperature outside the heating area was 23.3˚C, significantly lower compared to Aldabra Atoll (30.3˚C; range: 23.8–43.8˚C), and to the environmental temperature range at which tortoises maximize their activity in the wild ($T_{a\text{-}opt}$; 25.8–31.7˚C). The heating area exhibited a mean temperature of 36.3˚C, and tortoises that made use of the heating area were able to maintain a mean core body temperature (T_{bc}) of 30.0˚C, which was comparable to the T_{bc} of tortoises during ZRH summer and on Aldabra trials, and an improvement over the mean T_{bc} recorded during the ZRH winter trial (21.2˚C). However, the smaller individuals reached the upper limits of T_{bc} recommended for the species, probably due to heating pad temperatures above $T_{a\text{-}opt}$. We discuss current practices to provide external heating sources for tortoises and how this method can be used to provide an adequate thermal environment for large captive reptiles. Finally, we provide recommendations for the installation of artificial heating sources for tortoises and large reptiles.

Keywords: *animal welfare*; *captivity*; *husbandry*; *reptiles, thermal environment*

Resumen

En este artículo, evaluamos la efectividad de la instalación de un área de calentamiento (compuesta de un calentador de concreto en el suelo y lámparas para asolearse) en ayudar a la termorregulación en las tortugas gigantes de Aldabra (Aldabrachelys gigantea) en el Zoológico de Zürich, Suiza. Evaluamos los patrones de termorregulación de cinco tortugas (25–193 kg) durante la primavera (ZRH primavera), y comparamos esto con resultados publicados sobre las mismas tortugas que fueron observadas antes de la instalación del área de calentamiento (ZRH verano y ZRH invierno), y en tortugas silvestres en el atolón de Aldabra. La temperatura ambiental media fuera del área de calentamiento fue de 23.3˚C, significantemente más baja en comparación con el atolón de Aldabra (30.3˚C; rango de 23.8–43.8˚C), y a la temperatura ambiental a la que las tortugas maximizan su actividad en estado silvestre ($T_{a\text{-}opt}$; 25.8–31.7˚C). El área de calentamiento mostró una temperatura media de 36.3˚C, y las tortugas que usaron dicha área fueron capaces de mantener una temperatura corporal interna (T_{ci}) media de 30.0˚C, la cual fue comparable con la T_{ci} de las tortugas durante el ZRH verano y en Aldabra, y un mejoramiento sobre la T_{ci} media alcanzada durante el ZRH invierno (21.2˚C). No obstante, los individuos más pequeños alcanzaron los límites superiores de la T_{ci} recomendada para la especie, probablemente debido a las temperaturas del área de calentamiento más altas que la $T_{a\text{-}opt}$. Discutimos las prácticas que se utilizan para proveer fuentes de calentamiento externas para tortugas y cómo este método puede ser utilizado para proveer un ambiente térmico adecuado para reptiles de gran tamaño en cautiverio. Finalmente, proveemos recomendaciones para la instalación de fuentes de calor artificiales para tortugas y reptiles de gran tamaño.

Introduction

Tortoises (Testudinidae) are amongst the most threatened taxa in the world, and many conservation efforts include captive populations. For example, Aldabra giant tortoises (*Aldabrachelys gigantea*) almost suffered the same fate as other giant tortoise species in the western Indian Ocean, which went extinct due to over exploitation (Stoddart et al. 1979). Although populations are now considered stable in its endemic range on Aldabra Atoll (Turnbull et al. 2015), the possible repercussions of climate change, such a sea level rise, is a cause of conservation concern, especially for such a low-lying atoll. Moreover, Aldabra giant tortoises are increasingly being used as analogous species to substitute extinct giant tortoises to re-establish the ecological functions that have been lost (Hansen et al. 2010), and these efforts rely on animals reared in captivity (Griffiths et al. 2013). These, among other factors, highlight the importance of maintaining captive breeding populations.

Perhaps one of the most important considerations for captive tortoises (and reptiles in general) is providing an appropriate thermal environment for thermoregulation, as the variations in external environmental temperatures significantly influence the thermoregulation biology of ectotherms. As with other reptiles, the use of artificial heating sources, such as basking lamps and ground heating pads, are often employed to maintain adequate external temperatures for tortoises, especially in temperate places. However, satisfying the thermoregulatory requirements of tortoises and other reptiles in captivity is often challenging (Pough 1991), particularly due to the lack of species-specific information on their thermal requirements and thermoregulation patterns.

In a recent study on the thermoregulation biology of Aldabra giant tortoises in the wild (Aldabra) and in captivity (Zürich Zoo), Falcón et al. (2018; Chapter 4) provide insights into the thermoregulatory patterns and strategies exhibited by this species. The study revealed that wild *A. gigantea* experience mean environmental temperatures (T_a) of 30.3˚C (range: 23.8–43.8˚C), that tortoises maximize their activity at an environmental temperature range ($T_{a\text{-}opt}$) of 25.7–31.2˚C, and that they thermoregulate to maintain their mean core body temperatures (T_{bc}) at about 30˚C (range: 26.0–35.0˚C). Moreover, they reported that although tortoises at the Zürich Zoo are kept in a greenhouse environment with controlled temperature and

humidity (Masoala Forest exhibit), the thermal conditions of the environment during winter was lower when compared to temperatures experienced by tortoises in the wild.

In this study, we assessed the effect of providing an artificial heating area to Aldabra giant tortoises at the Masoala Rainforest exhibit in the Zürich Zoo during spring, consisting of a concrete heat pad and basking lamps, with tortoises being able to choose freely whether to use them, and recorded the tortoises' body temperature patterns in relation to environmental temperatures. To assess the effect of the installation of artificial heating sources, we compared the results of this study to those reported by Falcón et al. (2018; Chapter 4) prior to the installation of the heating area (during the ZRH winter and summer trials), and in the wild (Aldabra Atoll trial). We expected the heating area to enhance the thermal environment of the tortoises and to provide similar temperatures to those observed in the wild, and for tortoises to readily choose to use the heating area when environmental temperatures were below the preferred temperatures in the wild. Moreover, we expected that by having access to artificial heating sources, tortoises would be able to regulate the core body temperatures to more closely match the patterns observed in the wild. Finally, we used the data to investigate patterns of thermal inertia in relation to body mass in these tortoises.

Methods

Study site and heating system

The present study took place in a section of the Masoala Forest exhibit at Zürich Zoo, in the compartment where the Aldabra giant tortoises are housed. The Masoala Forest exhibit is a greenhouse ecosystem (11,000m^2) that has a translucent foil cover that allows 75% of daylight- and 50% UV radiation to penetrate, it has an air circulating and heating system, and artificial rain and fog systems (Bauert et al. 2007).

During the spring of 2013 (ZRH spring trial), a concrete ground heater and two basking lamps (TERM 2000 IP67 Quartzheat, Burda Worldwide Technologies, Eschborn, Germany) were installed in the tortoise enclosure at the Masoala Forest exhibit to increase the upper temperature range available to the tortoises (Fig. 1).

The lamps have a distance of 1.25-1.60 m above the heater, and are on a timed schedule that switches them off for 30 minutes after a 2-hour heating interval. The concrete ground heater was working continuously. The tortoises were free to choose to use the new heating system, with the exception of one male ("SBY") that was separated from the group for management reasons. This animal therefore served inadvertently as a control for the heating area treatment.

Thermal environment and thermoregulation of Aldabrachelys gigantea

To study the patterns of body temperature of Aldabra giant tortoises, we followed Falcón et al. (2018; Chapter 4), and monitored the same five individuals that were monitored in that study in Zürich Zoo. We used 11-bit HC temperature loggers (±0.06˚C accuracy; OnSolution Pty Ltd., NSW, Australia) to record environmental (T_a) and tortoise core body temperatures (T_{bc}) every 15 minutes. To record environmental temperatures, loggers were placed at two locations at a height between 0.3–0.5 m: a shaded area measuring air temperature (T_{air}) and an area exposed to the sun to record radiative temperature (T_{sun}). To record the core body temperatures of tortoises, we fed the loggers to the animals. In addition, external body temperatures (T_{be}; carapace, extremities and skinfolds) and temperatures of the heating area (on the concrete pad) were measured using an infrared thermometer pistol (*Raytek Fluke 566*; 0.01˚C accuracy; Raytek Corporation, Santa Cruz, USA); two additional females of 80 kg each were included in the temperature pistol measurements. The ground temperature of where the tortoises were located (the average of the temperatures taken on the left and right side directly next to the tortoise) as well as of the concrete heat pad was monitored in parallel to the animals' surface temperatures using the same infrared thermometer. Changes in ground temperature for an individual tortoise mainly represent changes of position (on or off the heat pad). During the course of the study, the animals had ad libitum access to drinking water, food, and access to both shade and sunlight, and to the artificial heating area. Food consisted of grass hay, freshly cut grass and vegetables.

Figure 1: Photo of the heating area in the tortoise enclosure of the Masoala Forest exhibit at Zürich Zoo. The heating area is between the camera and the Aldabra tortoises, consisting of a heater underneath the concrete surface and two basking lamps. Note that food is not placed on the heated area.

Statistical analyses

All statistical analyses were performed using R v. 3.3.3 (R Core Team 2017). Data was plotted using the R packages 'graphics' (native) and 'ggplot2' (Wickham 2016). To determine whether the environmental temperature and the tortoises' core body temperature patterns differed from those reported prior to the installation of the heating area in the tortoise enclosure in Zürich Zoo (ZRH spring trial compared to ZRH winter and summer trials), and from those reported for tortoises in the wild (Aldabra), we used the Kruskall-Wallis rank sum test. We then used Dunn's test of multiple comparisons using rank sums with Bonferroni correction (Dunn 2012; Hochberg 1988) to identify statistical differences between groups (package 'dunn.test'; Dinno 2016). For the statistical comparison and graphing of T_{bc} between trials, we removed tortoise "SBY" because it did not have access to the heating area during the ZRH spring trial.

To evaluate the effectiveness of temperature regulation, we followed Hertz et al. (1993), with modifications. To determine the index of the effectiveness of temperature regulation ($\tilde{}d_b$), one would calculate the degree by which the T_{bc} of tortoises deviate from their preferred core body temperature (T_{pref}; i.e., the range of core body temperatures within which an ectothermic animal seeks to maintain itself). Instead of T_{pref}, we used the environmental temperature range at which activity of Aldabra giant tortoises is maximized ($T_{a\text{-}opt}$), which was within the T_{pref} of other testudinid species, and envelops the range of T_{bc} exhibited by wild Aldabra giant tortoises (Falcón et al. 2018; Chapter 4) . The $\tilde{}d_b$ index measures the absolute value of the deviation of T_{bc} to $T_{a\text{-}opt}$ range, with departures from zero indicating the average degree to which the animals experience T_{bc} outside $T_{a\text{-}opt}$. Analogously, we calculated the deviations of the mean T_a from $T_{a\text{-}opt}$ for each trial as a measure of the thermal quality of the environment ($\tilde{}d_a$; see Hertz et al. 1993 for details). Because $\tilde{}d_b$ close to zero does not necessarily indicate active thermoregulation, we then we compared $\tilde{}d_b$ with the distribution of T_{bc} against T_a and the heater temperatures for each individual. For example, animals with a $\tilde{}d_b$ close to zero but that follow the patterns of environmental temperatures that are within their preferred range may be actually thermoconforming. We visualized this by performing kernel density estimations of the temperatures of the environment and the heating area in

comparison to the T_{bc} of tortoises (visualised with R package 'ggplot2'). Finally, to investigate the effect of body mass on thermal inertia, we plotted simultaneous measurements of the T_{be} of the carapace and the innermost skinfold against each other. A slope of 1 in this relationship would indicate that skinfold temperature follows carapace temperature immediately, i.e., a low degree of thermal inertia. Lower slopes (between 0 and 1) would indicate that skinfold temperature changes at a slower rate than carapace temperature; lower slopes hence denote a more prominent thermal inertia. We tested for a correlation of the mean slope per animal and body mass by a simple correlation analysis. The significance level was set to 0.05.

Results

Environmental temperatures ranged from 18.2–38.1˚C during the ZRH spring trial, and the mean temperature of the heating area was 36.3˚C (Table 1). The environmental temperatures (T_{sun} and T_{air}) were significantly different among trials, with ZRH spring trial temperatures being intermediate between ZRH winter and ZRH summer trials, and comparatively lower than on the Aldabra trial (Fig. 2a-b). The aggregated T_{bc} of tortoises was significantly different for all trials (Fig. 2c). The T_{bc} of tortoises during the ZRH summer trial were similar to those of tortoises on the Aldabra trial, but their T_{bc} during the ZRH winter trial was considerably lower. Moreover, the aggregated T_{bc} of tortoises during ZRH spring trial was slightly lower, and more variable, from that exhibited y tortoises during ZRH summer or on Aldabra trials. The two smaller tortoises exhibited higher T_{bc} when compared to those of the two bigger tortoises that had access to the heating area (Fig. 2d). followed the same pattern as, but lagged behind, environmental temperatures (Fig. 3). The mean T_{bc} for all tortoises combined was 30.0˚C, and it ranged from 22.2–36.1˚C (Table 1). During the first five days and the last three days of the trial, tortoises that had access to the heating area were able to maintain their T_{bc} oscillating around 30˚C despite low environmental temperatures. However, the individual SBY (140 kg), without access to the heating area, had consistently lower T_{bc} than the other animals at low environmental temperatures, achieved similar T_{bc} as the others when T_a increased temporarily, and dropped in T_{bc} again with after the warm spell (Fig. 3).

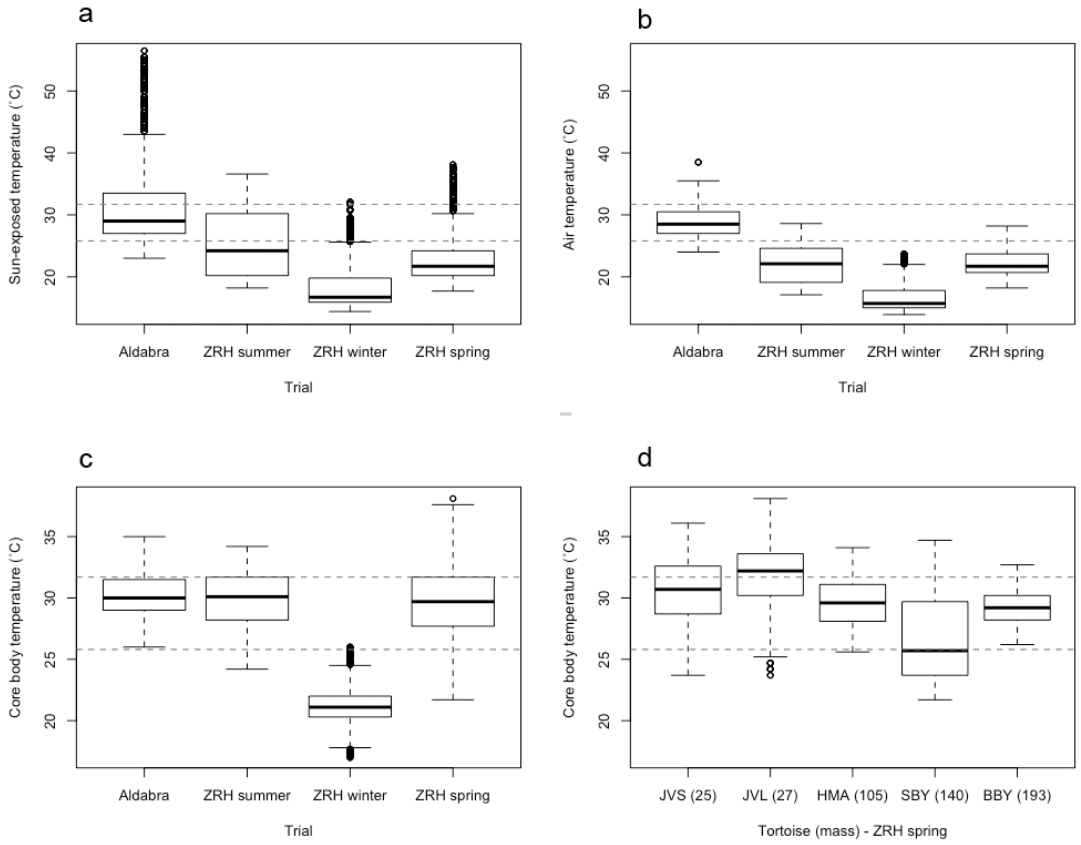

Figure 2: Comparison of environmental and core body temperatures experienced by Aldabra giant tortoises (*Aldabrachelys gigantea*) on the Aldabra Atoll trial, and Zürich Zoo prior and after the installation of an artificial heating area. The figure shows (a) temperatures in the sun-exposed areas (T_{sun}), (b) air temperatures (in shaded areas; T_{air}) and (c) the aggregated tortoise core body temperature (T_{bc}) per trial, and (d) the T_{bc} of tortoises during the ZRH spring trial. Tortoise "SBY" (140 kg) was the only tortoise that did not have access to the heating area, and was excluded from ZRH spring (in panel c). The gray dashed-lines depict the environmental temperature range at which wild Aldabra giant tortoises maximize their activity in the wild (25.8–31.7˚C). Except for T_{bc} in ZRH summer and ZRH spring, all groups/individuals within each plot (a–d) are statistically significant different according to Dunn's test of multiple comparisons using rank sums (at $p < 0.01$) after Kruskal-Wallis H test.

There was considerable variation in terms of the selection of the heating area between tortoises that had the ability to do so; yet, this generally resulted in higher core and external body temperatures when compared to tortoise "SBY" (which did not have access to the heating area; Fig. 4). In the latter figure, active selection of the heating area can be seen in tortoises that have a ground temperature (measured on the side of each tortoise) close-to that of the heating area (compared to tortoise "SBY", which showed ground temperatures within the range of T_{sun} and T_{air}).

Table 1: Summary statistics of environmental (T_a)- and tortoise core body (T_{bc}) temperatures during the ZRH spring trial, quality of thermal environment ($\tilde{}d_a$), and tortoise thermoregulation efficiency ($\tilde{}d_b$). Tortoise "SBY" did not have access to the heating area and therefore served inadvertently as a control for the heating area treatment.

***Environmental temperature* (T_a °C)**

Environment	Mean	±SD	Min	Max	$\tilde{}d_a$
Sun	23.1	4.6	17.7	38.1	5.7
Shade	22.1	2.2	18.2	28.2	6.7
Heater	36.3	2.3	31.8	40.2	7.6

***Tortoise core body temperature* (T_{bc} °C)**

Tortoise (mass)	Mean	±SD	Min	Max	$\tilde{}d_b$
JVS (25kg)	30.6	2.8	23.7	36.1	1.8
JVL (27kg)	31.6	2.5	23.7	35.6	2.8
HMA (105kg)	29.8	2.1	25.6	34.1	1.0
SBY (140kg)	26.7	3.5	21.7	34.7	2.1
BBY (194kg)	29.4	1.4	26.2	32.7	0.6

The thermal quality of environmental temperatures and the temperature of the heating area ($\tilde{}d_a$, i.e., the deviations from $T_{a\text{-}opt}$), ranged from 4.7–7.9 during the spring trial, and the mean $\tilde{}d_a$ (from T_{sun} and T_{air}) was comparatively lower when compared to the thermal environment in the wild (Table 2). In spite of this, tortoises that had access to the heating area were able to maintain an index of thermoregulation effectiveness ($\tilde{}d_b$) close to zero, and similar to the one exhibited during the summer and by tortoises on Aldabra. Moreover, the resulting aggregated $\tilde{}d_b$ during the spring trial was much lower than that exhibited by tortoises during the ZRH winter trial (Table 2). However, tortoise "SBY", which did not have access to the heating area, had a larger $\tilde{}d_b$ index when compared to the other two larger tortoises (Table 1), and similar to the smaller ones. When comparing the distribution of T_{bc} against T_a and the heater temperatures for each individual, it is clear that tortoises were thermoregulating (as opposed to thermoconforming; Fig. 5). In the latter figure, we can observe how tortoise "SBY" that did not have access to the heating had lower T_{bc}, and how the T_{bc} of the two smaller tortoises were closer to the temperatures of the heating areas when compared to the larger tortoises.

The relationship between the T_{be} of the carapace and the innermost skinfold was close to linearity in the smaller tortoises (both in spring, winter, and across both seasons combined). In contrast, the respective slopes were lower in larger animals (Fig. 6). There was a significant negative correlation between the slope of the carapace-skinfold relationship and the body mass of the respective tortoises (R = -0.98, p = 0.005, n = 5).

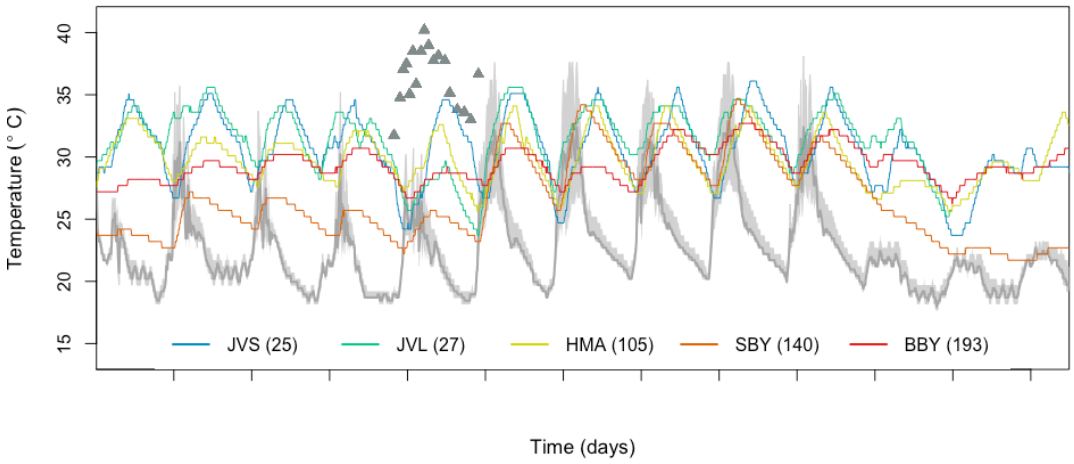

Figure 3: Environmental temperature (T_a) fluctuations and core body temperature (T_{bc}) fluctuations of Aldabra giant tortoises (*Aldabrachelys gigantea*) of different mass during the ZRH spring trial, after the installation of an artificial heating area. The mass of the tortoises is given in parenthesis (kg). The mean environmental temperature (and the range) are shown in grey, while the core body temperatures of tortoises are shown in colour (with warmer colours indicating larger mass). The concrete heater pad temperatures recorded with infrared thermometer are depicted by triangles. The x-axis intervals indicate a 24-hour period. Notice that tortoise 'SBY' did not have access to the heating area (orange line).

Discussion

Tortoises, as other ectotherms, are dependent on environmental temperature to regulate physiological processes and behaviour, which ultimately affect their growth, survival, and reproduction. For example, temperature is known to affect tortoise metabolic rate (Wood et al. 1978), growth rates and abnormalities such as carapacial scute pyramiding (Heinrich & Heinrich 2016), and susceptibility to cloacal infections (Samour et al. 1986). Thus, providing an adequate thermal environment for tortoises in captivity is of paramount importance.

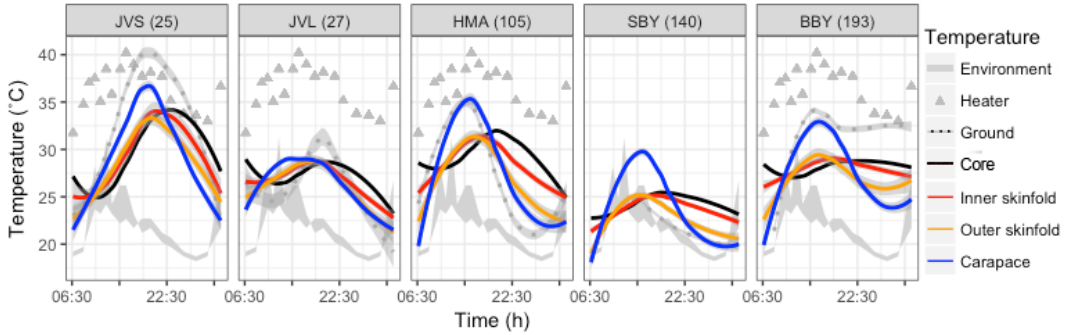

Figure 4: Hourly patterns of core (T_{bc}) and external (T_{be}) body temperature of Aldabra giant tortoises (*Aldabrachelys gigantea*) in relation to environmental temperatures during the ZRH spring trial. Notice how the ground temperature recorded for each tortoise reflect movement to and out of the heating area (except for tortoise "SBY", which did not have access to the heating area). Tortoise body mass is given in parenthesis (kg).

Here we studied how the installation of an artificial heating area affected the thermoregulation of Aldabra giant tortoises. In our study, a tortoise that was separated from the group for management reasons and did not have access to the heating area served as a control. Tortoises that had access to the heating area readily made use of it, and different from the control, they were able to maintain a T_{bc} that oscillated around 30˚C, which is similar to temperatures exhibited by wild tortoises (Falcón et al. 2018; Chapter 4). Moreover, they were able to maintain the overall distribution of T_{bc} within $T_{a\text{-}opt}$ despite pronounced drops in environmental temperatures (T_{air} and T_{sun}). Thus, our results demonstrate that providing supplementary heat via artificial sources enhances the thermal environment of tortoises and results in thermoregulatory patterns of T_{bc} similar to those exhibited by wild individuals.

However, several aspects require consideration. The temperature recorded directly on the heating area reached 40˚C, and tortoises that had access to the heating area, especially the smaller ones (≤25kg), exhibited T_{bc} values above the $T_{a\text{-}opt}$. The high temperatures and the oscillations observed may have been due to the combined effect of the basking lamps, heating pad and sun exposure, while the differential effect on tortoises of different mass may have been due to the effects of thermal inertia, where smaller animals do not only cool down, but also heat up at a faster rate. However, the T_{bc} remained within the range of upper T_{bc} observed in the wild (Falcón et al. 2018; Chapter 4), and the control tortoise also exhibited T_{bc} above

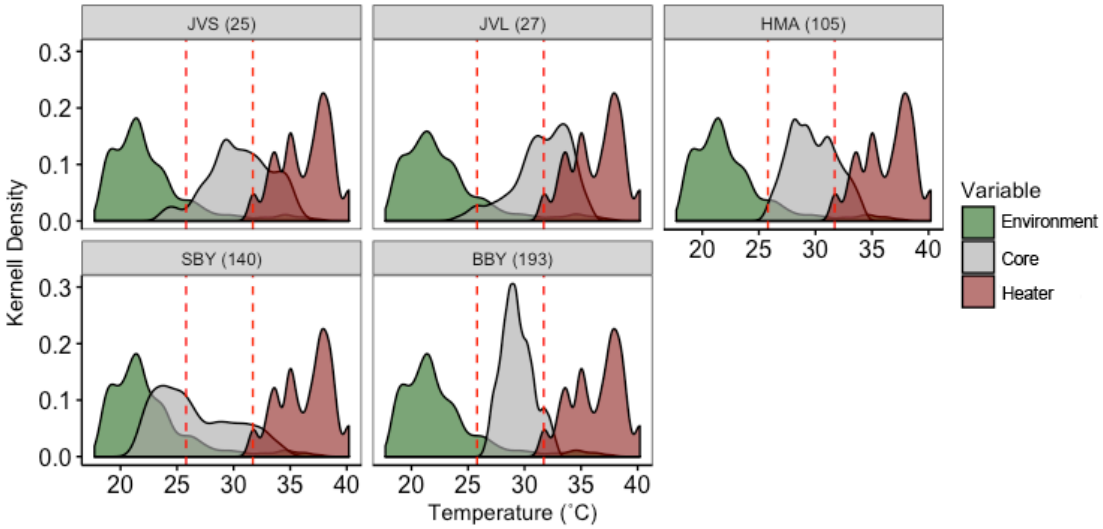

Figure 5: Core body temperatures (T_{bc}) of Aldabra giant tortoises (*Aldabrachelys gigantea*) during the ZRH spring trial, in relation to environmental (T_a) and heating area temperatures. The red dashed-lines depict the environmental temperature range at which wild Aldabra giant tortoises maximize their activity in the wild ($T_{a\text{-}opt}$; 25.8–31.7˚C). The distribution of T_{bc} independent from that of external temperatures is indicative of active thermoregulation, and distributions of T_{bc} within $T_{a\text{-}opt}$ is indicative of effective thermoregulation. Notice how tortoise "SBY", which did not have access to the heating area, maintained T_{bc} lower than that of other tortoises, but shows signatures of active thermoregulation. Environmental temperatures, T_a, are given by the combination of sun-exposed, T_{sun}, and air temperature, T_{air}.

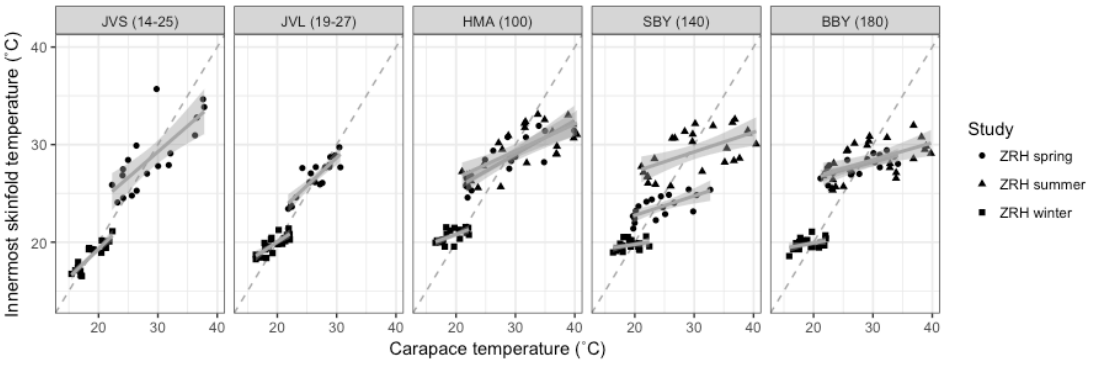

Figure 6: Relationship of the temperature of the outer carapace and the innermost skinfold next to the leg in Aldabra giant tortoises (*Aldabrachelys gigantea*) at the Zürich Zoo in three different trials (seasons), sorted by body mass. Note that the two youngest animals were not included in the summer study, and that animal "SBY" did not have access to the heating spot in spring, which resulted in generally lower temperatures. The slopes of the individual regression lines (solid lines) for each season are indicated. The broken line denotes y = x. Note lower slopes in larger individuals, indicative of thermal inertia.

$T_{a\text{-}opt}$ when exploiting environmental temperatures during the warm spell. Thus, the effects of the interplay between temperatures in the heating area and natural heat, as well as thermal inertia in tortoises must be considered when installing and maintaining artificial heating areas for the maintenance of T_{bc} within acceptable ranges.

There are several ways to provide an adequate thermal environment by using artificial heating sources to improve the welfare of reptiles in captivity. Basking species such as Aldabra giant tortoises can benefit from localized heating areas with basking lamps, which should provide temperatures as high as 45˚C (McArthur & Barrows 2008). However, basking lamps can be insufficient to heat up the ground and provide appropriate heating for basking species in temperate climates (which can lead to rapid heat loss through conduction), and result in low T_{bc} as well as cloacal infections in tortoises (Samour et al. 1986). Whether to include ground heating or not for a basking species, however, should not be taken lightly. For basking species over 25kg, ground heating in addition to heating from light sources is acceptable (McArthur & Barrows 2008), especially under conditions of low temperatures such as the ones observed during winter in Zürich Zoo. If ground heating is necessary for enclosures harbouring Aldabra giant tortoises, we recommend temperatures close-to the upper temperatures $T_{a\text{-}opt}$ (32˚C). When providing heating for tortoises, it is important to make sure that the tortoises have access to other areas to cool down, and to ensure that small animals cannot be trapped on the heating pad by larger conspecifics. Chelonians lack suitable pain receptors and appear to be unable to respond to heat trauma, so it is important to carefully monitor ground heating areas to avoid injuries and fatalities (McArthur & Barrows 2008).

Additionally, another solution could be to place heat pads on a vertical structure (e.g., side wall) to provide tortoises with radiant (rather than conductive) heat sources (McArthur & Barrows 2008). If possible, it would also be beneficial to simulate the daily patterns of environmental temperature change by adjusting the time and intensity at which artificial sources of heat are available, possibly using several artificial heat sources at different localities within an enclosure. Taking these

steps will ensure the wellbeing of the animals, and that the T_{bc} of tortoises remains within an acceptable range.

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GENERAL DISCUSSION

GENERAL DISCUSSION

Through the work I presented in my thesis, along with my collaborators, I studied the role of chelonians as frugivores and seed dispersers, from the individual and species level, to their position at the community level. I did this by reviewing the literature available of frugivory and seed dispersal by chelonians, and then focusing on Aldabra giant tortoises to assess different factors affecting their function as fruit consumers and seed dispersers on Aldabra Atoll, and their role in the plant–frugivore community on the atoll.

Although researchers in individual studies have highlighted the importance of chelonians in frugivory and seed dispersal (FSD), a review and synthesis was lacking. In **Chapter 1**, I reviewed and synthesised the information on the capabilities of chelonians as frugivores and seed dispersers. Chelonians have so far been largely ignored in the literature on seed dispersal ecology. I assessed the quality and quantity of chelonian seed dispersal, and their efficiency as dispersers in the many habitats across the world in which they occur. My findings suggest that chelonians likely outperform many of the other vertebrate seed dispersers in their communities, and will hopefully bring chelonians into the spotlight as efficient frugivores and seed dispersers.

Chapter 2 dealt with the role of Aldabra giant tortoises (*Aldabrachelys gigantea*) in the plant–frugivore community of Aldabra Atoll, and gaining an understanding of seed dispersal interactions at the community level. My study provides the first evaluation of the role of tortoises and other dispersers in the plant–frugivore community of Aldabra Atoll, and is the third study to date that evaluates the role of chelonians as seed dispersers at the community level using network analyses. Furthermore, to my knowledge, my study on the Aldabra seed dispersal network is the first of its kind performed in the Western Indian Ocean. I showed that Aldabra giant tortoises are central in the seed dispersal network (SDN) of the atoll, and the second most important frugivore in terms of the quantity of interactions, after the Comoros blue pigeon (*Alectroenas sganzini*). I also showed that tortoises, together with blue pigeons and Madagascan bulbuls (*Hypsipetes madagascariensis*), drive the seed dispersal network of Aldabra by forming a strong core structure that promotes network stability. Closely related species of these

frugivores have gone extinct on other islands in the western Indian Ocean, and there have been calls to restore these interactions (Kaiser-Bunbury et al. 2010). Our new understanding of the SDN of Aldabra has direct conservation implications for the functional resurrection of extinct seed dispersal interactions in the western Indian Ocean. The network can be used as a functional baseline to decide which of the recently extinct frugivores should be the focus of ongoing and planned rewilding efforts on other islands in the western Indian Ocean. Moreover, although the faunal and floral community of Aldabra is a recently assembled one (Braithwaite, Taylor, & Kennedy, 1973), my results show that its seed dispersal network still exhibited the invariant properties found in ecologically older networks (Bascompte et al. 2003; Olesen et al. 2007).

In **Chapter 3** I evaluated whether the body size of Aldabra giant tortoises and/or seed size affect the seed gut retention time (GRT) of tortoises. My study is one of the few that simultaneously evaluates the effects of both factors on seed GRT. I found that larger does not mean longer; that is, neither body size nor seed size affected the GRTs of tortoises. Studies on different species, including Aldabra giant tortoises, have previously found both similar and opposite results, with gut retention times of tortoises being affected by a myriad of factors (e.g., Bjorndal 1989; Hatt et al. 2002; Sadeghayobi et al. 2011; Varela & Bucher 2002; Waibel et al. 2013). It is not thus possible to draw general conclusions based on my results. However, assuming that my results are applicable to Aldabra giant tortoises in general, they suggest that both small and large tortoises are equally capable of retaining small and large seeds in their guts for 2–4 weeks. Therefore, from a seed dispersal point of view, small and large *A. gigantea* can be considered similarly useful in rewilding projects as taxon substitutes for recently extinct endemic giant tortoises. Indeed, seed dispersal is one of the most common extinct interactions that practitioners aim to resurrect to restore ecosystem functions (Griffiths et al. 2011; Hansen et al. 2008; Kaiser-Bunbury et al. 2010).

In **Chapter 4**, I evaluated the effects of environmental temperature on the activity and body temperature regulation of Aldabra giant tortoises. My work is the first to assess the thermoregulatory environment and ecology of Aldabra giant tortoises across temperature gradients. I showed how environmental temperature

affects the activity of giant tortoises, and identified the environmental temperature at which their activity was maximised. I then showed that Aldabra giant tortoises act as conformer-regulators that maintain their core body temperatures close to 30˚C, within the temperature range at which they maximise their activity. I also examined whether thermal inertia was a factor playing a role in the tortoises' body temperature regulation, and whether they exhibited inertial homeothermy due to their large size. I found that the presence of thermal inertia was more pronounced in colder environments, and that temperature stability associated with larger size was also only achieved in colder environments. These findings emphasise the environmental thermal context-dependency of tortoise thermoregulation, and the possible role of behavioural thermoregulation in overriding these effects. Despite being giants, I found no evidence for inertial homeothermy, supporting previous suggestions, by Grigg et al. (2004), that this is only possible for ectotherms with a body mass above 500 kg. I proposed that the values for preferred core temperature and the temperature range at which tortoises maximise their activity, can serve as baselines for the management of the thermal environment of these giants both for captive populations and in the wild, especially in an era of climate change.

This is exactly what I did in **Chapter 5**, where I provided a case study on how to effectively manage the thermal environment of captive Aldabra giant tortoises in the Zürich Zoo. Using the methods and findings from the previous chapter, I could evaluate whether the provision of artificial heating sources resulted in similar thermoregulatory patterns as those found in the wild. Indeed, I found that even under suboptimal, low environmental temperatures, if tortoises were offered heating sources providing the temperature ranges at which they maximise their activity in the wild, they were capable of regulating their core body temperatures close to 30˚C, as observed in wild individuals.

To conclude, along with my collaborators, I was able to show the capabilities and the importance of turtles and tortoises as frugivores and seed dispersers in different habitats around the world, which will hopefully inspire others to further our understanding of the role that chelonians play as seed dispersers, especially at the community level. I also added support to the notion that the megafaunal giant tortoises are important ecosystem engineers and keystone species, by

demonstrating their capabilities as seed dispersers and their crucial role in the plant–frugivore community of Aldabra Atoll. In addition, my work set a baseline for managing the thermal environment in natural, rewilded and captive populations of Aldabra giant tortoises, which are increasingly being used for restoration. Finally, my work allowed me to greatly advance our understanding of the complex network of plant–frugivore interactions that occur on Aldabra Atoll.

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I have to start with Raymond L. Tremblay, who, despite working mainly on orchids at the moment, listened to me jabbering away my proposal to study invasive parakeets while I was an undergraduate student. With him, I learned a lot about population ecology, statistics, funky music, to love orchids, and got hooked up with 'proper coffee for an aspiring researcher' (the good stuff, not drip or instant coffee). During my work at Raymond's lab, I had the opportunity to participate in different research programs that aimed to promote students to pursue graduate studies, and they definitely had an impact on my decision to pursue my master's and doctoral studies: The Puerto Rico Louis Stokes Alliance for Minority Participation, the Center for Applied Tropical Ecology and Conservation, and the McNair Scholars Program. I am grateful for the opportunities they provided me. I also have to thank the professors and staff of the Department of Biology at the University of Puerto Rico at Humacao, who endured my excitement for ecology, encouraged me to participate in internships, and helped me through my years at the university. Especially, I thank Dr. Maritza Reyes, Director of the McNair Scholar Program, for approaching me during a poster presentation and asking me to join the program. The program, and her guidance, resulted in both personal and professional development that served me when applying to graduate school.

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As you may have noticed, I have been very lucky in getting great mentors, and this luck followed me to my PhD. I was already applying to two doctoral programs, when an email about a PhD position working with giant tortoises caught my eye. I was infatuated with working on genetics at the moment–something the project did not include–and I sent an email to Dennis M. Hansen to inquire whether integrating work on tortoise genetics to the project was possible (and sent my CV). Unfortunately, and due to the scope of the work, this was not possible, but Dennis told me that I should apply for the position nonetheless. After reading a short description, and because it didn't include genetics, I put it as 'my third option'. After some time, I made it to the short list, and received the full description of the project, which involved working on Aldabra Atoll. I fell in love with the project! Suddenly my 'third option' became the first. I met Dennis during the winter of 2012 for the interview, and besides having to get used to looking up when talking to him (because he is bloody tall), I felt (here comes the cliché) a 'click'. I obviously ended up getting the position, and my work with Dennis officially began in 2013. Through the years, Dennis not only became my mentor, but truly an 'academic father'. If it wasn't for his endless support and understanding, I would not have reached this stage in my academic career. For guiding me during all these years, enduring my digressions, and having the occasional tortoise poop fight with me on Aldabra, I thank you. "Wiremesh, wiremesh…" –internal joke.

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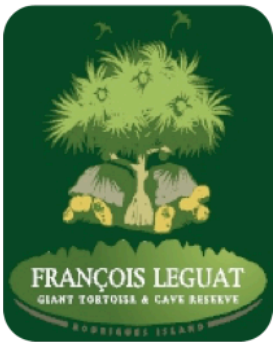
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Christina de Jesús Villanueva: “The origin and genetic structure of invasive green iguana (*Iguana iguana*) in Puerto Rico”; MSc received in 2016 from the University of Puerto Rico (served as external advisor).

Awards

José Ramón Ortíz awardee (2013): Awarded to the student with the highest GPA upon graduation in the MSc Biology Program.

Fulbright US Student Program (2013): Recommended by the US National Screening Committee of the Institute of International Education for studies in New Zealand.

Bridge to the doctorate fellow (2010–2012): 2-year competitive fellowship sponsored by the US-NSF that included salary, and research/travel funding.

Antarctica Service Medal of the USA (2010): Awarded to personnel serving in the US Antarctic Program and stationed in the continent.

USDA Faculty and Student Teams Program fellow (2010): Competitive fellowship placing a faculty and two students from Hispanic Serving Institutes in selected National Research Initiatives. Dr. Curt Daehler was our host Faculty during our training on Species Distribution Modelling in the University of Hawai'i - Mãnoa.

Ronald E. McNair scholar (2008–2010): A US Federal TRIO program that provides competitive scholarships with the aim to prepare undergraduates for doctoral studies.

Scholarly Service

Journal referee: *Annals of Botany*, *Biological Invasions*, *Herpetological Conservation and Biology*, *Integrative Zoology*, and *Pacific Science*.

Invited lecture: “The role of trade in biological invasions: The green iguana invasion as a case study”. Presented at the Invasive Species Ecology undergraduate course taught by Dr. James D. Ackerman at the University of Puerto Rico.

Publications

Falcón, W, and RL Tremblay. *In review*. From the cage to the wild: Introductions of Psittaciformes to Puerto Rico with emphasis on the invasive ecology of the white-winged parakeet. *Avian Biology*.

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APPENDICES

APPENDICES

Appendix 1: Full references for the literature and sources of information related to chelonian frugivory and seed dispersal, gut retention times, home range and movement, and germination success reviewed in this article.

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Appendix 2: Chelonian species that engage in frugivory and seed dispersal, and the species of plants that they consumed and/or disperse.

Reference	Chelonian species	Plant species
Amorocho and Reina 2008	*Chelonia mydas*	*Rhizophora mangle*
Andriantsaralaza et. al. 2013	*Aldabrachelys gigantea*	*Adansonia fony*
Armstrong and Booth 2005	*Elseya albagula*	*Costanospermum australe*
Arthur et. al. 2008	*Chelonia mydas*	Unidentified 'mangrove'
Auffenberg and Weaver 1969	*Gopherus berlandieri*	*Aristida* sp.
Auffenberg and Weaver 1969	*Gopherus berlandieri*	*Aster* sp.
Auffenberg and Weaver 1969	*Gopherus berlandieri*	*Buchloe* sp.
Auffenberg and Weaver 1969	*Gopherus berlandieri*	*Celtis pallida*
Auffenberg and Weaver 1969	*Gopherus berlandieri*	*Cenchrus* sp.
Auffenberg and Weaver 1969	*Gopherus berlandieri*	*Chloris* sp.
Auffenberg and Weaver 1969	*Gopherus berlandieri*	*Citharexylum* sp.
Auffenberg and Weaver 1969	*Gopherus berlandieri*	*Plantago* sp.
Auffenberg and Weaver 1969	*Gopherus berlandieri*	*Viola* sp.
Auffenberg and Weaver 1969	*Gopherus berlandieri*	*Xanthophyllum* sp.
Auffenberg and Weaver 1969	*Gopherus berlandieri*	*Cylindropuntia leptocaulis*
Auffenberg and Weaver 1969	*Gopherus berlandieri*	*Opuntia engelmannii*
Ayres et. al. 2010	*Emys orbicularis*	*Nymphaea alba*
Balensiefer and Vogt 2006	*Podocnemis unifilis*	*Eichhornia* sp.
Balensiefer and Vogt 2006	*Podocnemis unifilis*	*Pistia* sp.
Balensiefer and Vogt 2006	*Podocnemis unifilis*	*Pseudobombax munguba*
Balensiefer and Vogt 2006	*Podocnemis unifilis*	*Salvinia sp.*
Balensiefer and Vogt 2006	*Podocnemis unifilis*	Unidentified Sapindaceae
Balensiefer and Vogt 2006	*Podocnemis unifilis*	Unidentified Poaceae
Balensiefer and Vogt 2006	*Podocnemis unifilis*	Unidentified Myrtaceae
Balensiefer and Vogt 2006	*Podocnemis unifilis*	Unidentified Melastomataceae
Balensiefer and Vogt 2006	*Podocnemis unifilis*	Unidentified Fabaceae
Balensiefer and Vogt 2006	*Podocnemis unifilis*	Unidentified Fabaceae
Balensiefer and Vogt 2006	*Podocnemis unifilis*	Unidentified Bombacaceae
Birkhead et. al. 2005	*Gopherus polyphemus*	*Acalypha gracilens*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Ambrosia* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Asclepias* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Commelina erecta*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Crataegus* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Digitaria* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Dyschoriste oblongifolia*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Gaillardia aestivalis*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Hypericum* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Licania michauxii*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Mollugo verticillata*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Oenothera* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Opuntia humifusa*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Oxalis* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Panicum* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Paspalum* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Physalis heterophylla*

Birkhead et. al. 2005	*Gopherus polyphemus*	*Plantago* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Polygala* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Polygonum* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Prunus angustifolia*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Prunus* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Rhynchospora* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Rubus* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Rumex* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Sclerodactylon macrostachyum*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Stellaria media*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Tradescantia ohiensis*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Tragia urens*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Veronica hederifolia*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Zornia bracteata*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Ipomoea* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Stylosanthes biflora*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Asimina angustifolia*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Passiflora edulis*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Piriqueta cistoides*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Mimosa quadrivalvis*
Birkhead et. al. 2005	*Gopherus polyphemus*	*Diodia* sp.
Birkhead et. al. 2005	*Gopherus polyphemus*	*Richardia* sp.
Blake et. al. 2012	*Chelonoidis nigra*	*Anthephora hermaphrodita*
Blake et. al. 2012	*Chelonoidis nigra*	*Blainvillea dichotoma*
Blake et. al. 2012	*Chelonoidis nigra*	*Brickellia diffusa*
Blake et. al. 2012	*Chelonoidis nigra*	*Cenchrus platyacanthus*
Blake et. al. 2012	*Chelonoidis nigra*	*Commelina diffusa*
Blake et. al. 2012	*Chelonoidis nigra*	*Cordia lutea*
Blake et. al. 2012	*Chelonoidis nigra*	*Crotalaria pumila*
Blake et. al. 2012	*Chelonoidis nigra*	*Cynodon dactylon*
Blake et. al. 2012	*Chelonoidis nigra*	*Cyperus ligularis*
Blake et. al. 2012	*Chelonoidis nigra*	*Desmodium incanum*
Blake et. al. 2012	*Chelonoidis nigra*	*Digitaria setigera*
Blake et. al. 2012	*Chelonoidis nigra*	*Eleocharis maculosa*
Blake et. al. 2012	*Chelonoidis nigra*	*Eleusine indica*
Blake et. al. 2012	*Chelonoidis nigra*	*Eriochloa pacifica*
Blake et. al. 2012	*Chelonoidis nigra*	*Hippomane mancinella*
Blake et. al. 2012	*Chelonoidis nigra*	*Ipomoea triloba*
Blake et. al. 2012	*Chelonoidis nigra*	*Kyllinga brevifolia*
Blake et. al. 2012	*Chelonoidis nigra*	*Opuntia echios*
Blake et. al. 2012	*Chelonoidis nigra*	*Panicum dichotomiflorum*
Blake et. al. 2012	*Chelonoidis nigra*	*Panicum maximum*
Blake et. al. 2012	*Chelonoidis nigra*	*Paspalum conjugatum*
Blake et. al. 2012	*Chelonoidis nigra*	*Passiflora edulis*
Blake et. al. 2012	*Chelonoidis nigra*	*Physalis pubescens*
Blake et. al. 2012	*Chelonoidis nigra*	*Pisonia floribunda*
Blake et. al. 2012	*Chelonoidis nigra*	*Polygonum opelousanum*
Blake et. al. 2012	*Chelonoidis nigra*	*Portulaca oleracea*
Blake et. al. 2012	*Chelonoidis nigra*	*Psidium galapageium*

Blake et. al. 2012	*Chelonoidis nigra*	*Psidium guajava*
Blake et. al. 2012	*Chelonoidis nigra*	*Rubus niveus*
Blake et. al. 2012	*Chelonoidis nigra*	*Scleria distans*
Blake et. al. 2012	*Chelonoidis nigra*	*Scleria hirtella*
Blake et. al. 2012	*Chelonoidis nigra*	*Sida rhombifolia*
Blake et. al. 2012	*Chelonoidis nigra*	*Sida spinosa*
Blake et. al. 2012	*Chelonoidis nigra*	*Sida spinosa*
Blake et. al. 2012	*Chelonoidis nigra*	*Solanum americanum*
Blake et. al. 2012	*Chelonoidis nigra*	*Stachytarpheta cayennensis*
Blake et. al. 2012	*Chelonoidis nigra*	*Synedrella nodiflora*
Blake et. al. 2012	*Chelonoidis nigra*	*Tradescantia fluminensis*
Blake et. al. 2012	*Chelonoidis nigra*	*Zanthoxylum fagara*
Blake et. al. 2012	*Chelonoidis nigra*	*Acacia rorudia*
Blake et. al. 2012	*Chelonoidis nigra*	*Bidens* sp.
Blake et. al. 2012	*Chelonoidis nigra*	*Galactia striata*
Blake et. al. 2012	*Chelonoidis nigra*	*Clerodendrum villosum*
Blake et. al. 2012	*Chelonoidis nigra*	*Brachiaria multiculma*
Blake et. al. 2012	*Chelonoidis nigra*	*Brachiaria mutica*
Blake et. al. 2012	*Chelonoidis nigra*	*Hippomane mancinella*
Blake et. al. 2012	*Chelonoidis nigra*	*Opuntia echios*
Blake et. al. 2012	*Chelonoidis nigra*	*Passiflora edulis*
Blake et. al. 2012	*Chelonoidis nigra*	*Psidium galapageium*
Blake et. al. 2012	*Chelonoidis nigra*	*Psidium guajava*
Blake et. al. 2015	*Chelonoidis nigra*	*Anthephora hermaphrodita*
Blake et. al. 2015	*Chelonoidis nigra*	*Axonopus micay*
Blake et. al. 2015	*Chelonoidis nigra*	*Blainvillea dichotoma*
Blake et. al. 2015	*Chelonoidis nigra*	*Brickellia diffusa*
Blake et. al. 2015	*Chelonoidis nigra*	*Cenchrus platyacanthus*
Blake et. al. 2015	*Chelonoidis nigra*	*Cordia lutea*
Blake et. al. 2015	*Chelonoidis nigra*	*Cyperus ligularis*
Blake et. al. 2015	*Chelonoidis nigra*	*Desmodium glabrum*
Blake et. al. 2015	*Chelonoidis nigra*	*Desmodium incanum*
Blake et. al. 2015	*Chelonoidis nigra*	*Digitaria setigera*
Blake et. al. 2015	*Chelonoidis nigra*	*Eleocharis maculosa*
Blake et. al. 2015	*Chelonoidis nigra*	*Eleusine indica*
Blake et. al. 2015	*Chelonoidis nigra*	*Eragrostis cilianensis*
Blake et. al. 2015	*Chelonoidis nigra*	*Eriochloa pacifica*
Blake et. al. 2015	*Chelonoidis nigra*	*Hippomane mancinella*
Blake et. al. 2015	*Chelonoidis nigra*	*Ipomoea triloba*
Blake et. al. 2015	*Chelonoidis nigra*	*Opuntia echios*
Blake et. al. 2015	*Chelonoidis nigra*	*Panicum dichotomiflorum*
Blake et. al. 2015	*Chelonoidis nigra*	*Panicum maximum*
Blake et. al. 2015	*Chelonoidis nigra*	*Paspalum conjugatum*
Blake et. al. 2015	*Chelonoidis nigra*	*Passiflora edulis*
Blake et. al. 2015	*Chelonoidis nigra*	*Pennisetum purpureum*
Blake et. al. 2015	*Chelonoidis nigra*	*Physalis pubescens*
Blake et. al. 2015	*Chelonoidis nigra*	*Pisonia floribunda*
Blake et. al. 2015	*Chelonoidis nigra*	*Polygonum opelousanum*
Blake et. al. 2015	*Chelonoidis nigra*	*Portulaca oleracea*

Blake et. al. 2015	*Chelonoidis nigra*	*Psidium galapageium*
Blake et. al. 2015	*Chelonoidis nigra*	*Psidium guajava*
Blake et. al. 2015	*Chelonoidis nigra*	*Rubus niveus*
Blake et. al. 2015	*Chelonoidis nigra*	*Scleria distans*
Blake et. al. 2015	*Chelonoidis nigra*	*Scleria hirtella*
Blake et. al. 2015	*Chelonoidis nigra*	*Sida rhombifolia*
Blake et. al. 2015	*Chelonoidis nigra*	*Sida salviifolia*
Blake et. al. 2015	*Chelonoidis nigra*	*Silene dichotoma*
Blake et. al. 2015	*Chelonoidis nigra*	*Solanum ochraceo-ferrugineum*
Blake et. al. 2015	*Chelonoidis nigra*	*Stachytarpheta cayennensis*
Blake et. al. 2015	*Chelonoidis nigra*	*Synedrella nodiflora*
Blake et. al. 2015	*Chelonoidis nigra*	*Tradescantia fluminensis*
Blake et. al. 2015	*Chelonoidis nigra*	*Zanthoxylum fagara*
Blake et. al. 2015	*Chelonoidis nigra*	*Acacia rorudia*
Blake et. al. 2015	*Chelonoidis nigra*	*Bidens sp.*
Blake et. al. 2015	*Chelonoidis nigra*	*Clerodendrum villosum*
Bonin et. al. 2006	*Batagur baska*	*Sorocea* sp.
Bonin et. al. 2006	*Batagur borneonensis*	Unidentified 'mangrove'
Bonin et. al. 2006	*Carettochelys insculpta*	*Pandanus aquaticus*
Bonin et. al. 2006	*Carettochelys insculpta*	*Syzygium forte*
Bonin et. al. 2006	*Chelonoidis denticulata*	*Jacaratia spinosa*
Bonin et. al. 2006	*Kinosternon baurii*	Unidentified Arecaceae
Bonin et. al. 2006	*Kinosternon scorpioides*	Unidentified Arecaceae
Bonin et. al. 2006	*Macrochelys temminckii*	*Quercus* sp.
Bonin et. al. 2006	*Mesoclemmys nasuta*	*Philodendron* sp.
Bonin et. al. 2006	*Trionyx triunguis*	*Phoenix* sp.
Bonin et. al. 2006	*Emydura subglobosa*	*Pandanus* sp.
Braun and Brooks 1987	*Terrapene carolina*	*Podophyllum peltatum*
Braun and Brooks 1987	*Terrapene carolina*	*Podophyllum peltatum*
Braun and Brooks 1987	*Terrapene carolina*	*Rubus* sp.
Braun and Brooks 1987	*Terrapene carolina*	*Vaccinium* sp.
Braun and Brooks 1987	*Terrapene carolina*	*Viburnum* sp.
Braun and Brooks 1987	*Terrapene carolina*	*Vitis rotundifolia*
Braun and Brooks 1987	*Terrapene carolina*	*Arisaema triphyllum*
Braun and Brooks 1987	*Terrapene carolina*	*Duchesnea indica*
Braun and Brooks 1987	*Terrapene carolina*	*Fragaria virginiana*
Braun and Brooks 1987	*Terrapene carolina*	*Gaylussacia baccata*
Braun and Brooks 1987	*Terrapene carolina*	*Morus alba*
Braun and Brooks 1987	*Terrapene carolina*	*Phytolacca americana*
Braun and Brooks 1987	*Terrapene carolina*	*Podophyllum peltatum*
Braun and Brooks 1987	*Terrapene carolina*	*Podophyllum peltatum*
Braun and Brooks 1987	*Terrapene carolina*	*Prunus* sp.
Braun and Brooks 1987	*Terrapene carolina*	*Rosa multiflora*
Braun and Brooks 1987	*Terrapene carolina*	*Rubus phoenicolasius*
Braun and Brooks 1987	*Terrapene carolina*	*Rubus* sp.
Braun and Brooks 1987	*Terrapene carolina*	*Vaccinium vacillans*
Braun and Brooks 1987	*Terrapene carolina*	*Vitis aestivalis*
Braun and Brooks 1987	*Terrapene carolina*	*Vitis rotundifolia*
Braun and Brooks 1987	*Terrapene carolina*	*Vitis vulpina*

Braun and Brooks 1987	*Terrapene carolina*	*Passiflora edulis*
Burgin and Renshaw 2008	*Chelodina longicollis*	*Eleocharis acuta*
Burgin and Renshaw 2008	*Chelodina longicollis*	*Eleocharis* sp.
Burgin and Renshaw 2008	*Chelodina longicollis*	*Gahnia* sp.
Burgin and Renshaw 2008	*Chelodina longicollis*	*Juncus* sp.
Burgin and Renshaw 2008	*Chelodina longicollis*	*Paspalum dilatatum*
Burgin and Renshaw 2008	*Chelodina longicollis*	*Polygonum* sp.
Burgin and Renshaw 2008	*Chelodina longicollis*	*Potamogeton* sp.
Burgin and Renshaw 2008	*Chelodina longicollis*	*Sagittaria graminea*
Burgin and Renshaw 2008	*Chelodina longicollis*	*Scirpus* sp.
Calviño-Cancela et. al. 2007	*Emys orbicularis*	*Nymphaea alba*
Caputo and Vogt 2008	*Phrynops rufipes*	*Bactris* sp.
Caputo and Vogt 2008	*Phrynops rufipes*	*Iriartella setigera*
Caputo and Vogt 2008	*Phrynops rufipes*	*Mauritia flexuosa*
Caputo and Vogt 2008	*Phrynops rufipes*	*Mauritia flexuosa*
Caputo and Vogt 2008	*Phrynops rufipes*	*Oenocarpus bataua*
Caputo and Vogt 2008	*Phrynops rufipes*	*Socratea exorrhiza*
Caputo and Vogt 2008	*Phrynops rufipes*	*Socratea exorrhiza*
Caputo and Vogt 2008	*Phrynops rufipes*	Unidentified Sapotaceae
Caputo and Vogt 2008	*Phrynops rufipes*	Unidentified Rubiaceae
Caputo and Vogt 2008	*Phrynops rufipes*	Unidentified Malvaceae
Caputo and Vogt 2008	*Phrynops rufipes*	Unidentified Fabaceae
Caputo and Vogt 2008	*Phrynops rufipes*	Unidentified Clusiaceae
Caputo and Vogt 2008	*Phrynops rufipes*	Unidentified Arecaceae
Caputo and Vogt 2008	*Phrynops rufipes*	*Euterpe precatoria*
Carlson et. al. 2003	*Gopherus polyphemus*	*Digitaria sp.*
Carlson et. al. 2003	*Gopherus polyphemus*	*Diodella teres*
Carlson et. al. 2003	*Gopherus polyphemus*	*Euphorbia maculata*
Carlson et. al. 2003	*Gopherus polyphemus*	*Licania michauxii*
Carlson et. al. 2003	*Gopherus polyphemus*	*Paspalum notatum*
Carlson et. al. 2003	*Gopherus polyphemus*	*Paspalum setaceum*
Carlson et. al. 2003	*Gopherus polyphemus*	*Quercus geminata*
Carlson et. al. 2003	*Gopherus polyphemus*	*Paspalum notatum*
Carlson et. al. 2003	*Gopherus polyphemus*	*Paspalum setaceum*
Cobo and Reu 1988	*Testudo graeca*	*Agrostis sp.*
Cobo and Reu 1988	*Testudo graeca*	*Anthoxanthum ovatum*
Cobo and Reu 1988	*Testudo graeca*	*Briza maxima*
Cobo and Reu 1988	*Testudo graeca*	*Briza minor*
Cobo and Reu 1988	*Testudo graeca*	*Carduus meonanthus*
Cobo and Reu 1988	*Testudo graeca*	*Carduus* sp.
Cobo and Reu 1988	*Testudo graeca*	*Cerastium glomeratum*
Cobo and Reu 1988	*Testudo graeca*	*Corynephorus* sp.
Cobo and Reu 1988	*Testudo graeca*	*Cynodon dactylon*
Cobo and Reu 1988	*Testudo graeca*	*Erodium* sp.
Cobo and Reu 1988	*Testudo graeca*	*Halimium halimifolium*
Cobo and Reu 1988	*Testudo graeca*	*Hypochaeris glabra*
Cobo and Reu 1988	*Testudo graeca*	*Isolepis* sp.
Cobo and Reu 1988	*Testudo graeca*	*Juncus* sp.
Cobo and Reu 1988	*Testudo graeca*	*Leontodon taraxacoides*

Cobo and Reu 1988	*Testudo graeca*	*Malcolmia lacera*
Cobo and Reu 1988	*Testudo graeca*	*Moenchia erecta*
Cobo and Reu 1988	*Testudo graeca*	*Ononis* sp.
Cobo and Reu 1988	*Testudo graeca*	*Panicum repens*
Cobo and Reu 1988	*Testudo graeca*	*Paspalum* sp.
Cobo and Reu 1988	*Testudo graeca*	*Polypogon maritimus*
Cobo and Reu 1988	*Testudo graeca*	*Ranunculus sardous*
Cobo and Reu 1988	*Testudo graeca*	*Ranunculus* sp.
Cobo and Reu 1988	*Testudo graeca*	*Reseda media*
Cobo and Reu 1988	*Testudo graeca*	*Rubus ulmifolius*
Cobo and Reu 1988	*Testudo graeca*	*Rumex bucephalophorus*
Cobo and Reu 1988	*Testudo graeca*	*Simaba* sp.
Cobo and Reu 1988	*Testudo graeca*	*Spergula arvensis*
Cobo and Reu 1988	*Testudo graeca*	*Sporobolus* sp.
Cobo and Reu 1988	*Testudo graeca*	*Vulpia* sp.
Cobo and Reu 1988	*Testudo graeca*	*Lotus subbiflorus*
Cobo and Reu 1988	*Testudo graeca*	*Ornithophus sativus*
Cobo and Reu 1988	*Testudo graeca*	*Astragalus pelecinus*
Cobo and Reu 1988	*Testudo graeca*	*Bromus rigidus*
Cobo and Reu 1988	*Testudo graeca*	*Briza maxima*
Cobo and Reu 1988	*testudo graeca*	*Hypochaeris glabra*
Cobo and Reu 1988	*Testudo graeca*	*Rumex bucephalophorus*
Cobo and Reu 1988	*Testudo graeca*	*Spergula arvensis*
Cobo and Reu 1988	*Testudo graeca*	*Anagallis arvensis*
da Costa 2012	*Podocnemis expansa*	*Pouteria elegans*
da Costa 2012	*Podocnemis expansa*	*Psidium* sp.
da Costa 2012	*Podocnemis expansa*	*Oryza* sp.
da Costa 2012	*Podocnemis expansa*	*Duroia* sp.
da Costa 2012	*Podocnemis expansa*	Unidentified
da Costa 2012	*Podocnemis expansa*	Unidentified
da Costa 2012	*Podocnemis expansa*	Unidentified
Deepak 2011	*Indotestudo travancorica*	*Artocarpus* sp.
Deepak 2011	*Indotestudo travancorica*	*Dillenia pentagyna*
Deepak 2011	*Indotestudo travancorica*	*Dillenia pentagyna*
Deepak 2011	*Indotestudo travancorica*	*Ficus virens*
Deepak 2011	*Indotestudo travancorica*	*Gomphandra sp.*
Deepak 2011	*Indotestudo travancorica*	*Grewia tiliifolia*
Deepak 2011	*Indotestudo travancorica*	*Lantana camara*
de Lima et. al. 1997	*Phrynops rufipes*	*Euterpe precatoria*
de Lima et. al. 1997	*Phrynops rufipes*	*Iriartella sp.*
de Lima et. al. 1997	*Phrynops rufipes*	*Oenocarpus bacaba*
de Lima et. al. 1997	*Phrynops rufipes*	*"Munbaca"* sp.
de Lima et. al. 1997	*Phrynops rufipes*	*"Pupunharana"* sp.
de Lima et. al. 1997	*Phrynops rufipes*	*Socratea exorrhiza*
de Lima et. al. 1997	*Phrynops rufipes*	*Oenocarpus bataua*
de Lima et. al. 1997	*Phrynops rufipes*	Unidentified Humiriaceae
de Lima et. al. 1997	*Phrynops rufipes*	Unidentified Fabaceae
de Lima et. al. 1997	*Phrynops rufipes*	Unidentified Euphorbiaceae
de Lima et. al. 1997	*Phrynops rufipes*	Unidentified [Annonaceae

del Vecchio et. al. 2011	*Testudo hermanni*	*Carduus pycnocephalus*
del Vecchio et. al. 2011	*Testudo hermanni*	*Hedera helix*
del Vecchio et. al. 2011	*Testudo hermanni*	*Rubus ulmifolius*
del Vecchio et. al. 2011	*Testudo hermanni*	*Ruscus aculeatus*
del Vecchio et. al. 2011	*Testudo hermanni*	Unidentified Fabaceae
de Neira and Johnson 1985	*Chelonoidis nigra*	*Psidium galapageium*
Elbers and Moll 2011	*Macrochelys temminckii*	*Diospyros virginiana*
Elbers and Moll 2011	*Macrochelys temminckii*	*Nyssa aquatica*
Elbers and Moll 2011	*Macrochelys temminckii*	*Quercus phellos*
Ellis-Soto et. al. 2017	*Chelonoidis donfaustoi*	*Passiflora edulis*
Ellis-Soto et. al. 2017	*Chelonoidis donfaustoi*	*Psidium guajava*
Ellis-Soto et. al. 2017	*Chelonoidis porteri*	*Passiflora edulis*
Ellis-Soto et. al. 2017	*Chelonoidis porteri*	*Psidium guajava*
Elsey 2006	*Macrochelys temminckii*	*Quercus sp.*
Evenden 1948	*Actinemys marmorata*	*Nuphar polysepala*
Fachín-Terán 1995 et. al.	*Mesoclemmys raniceps*	Unidentified Fabaceae
Fachín-Terán 1995 et. al.	*Mesoclemmys raniceps*	Unidentified Myrtaceae
Fachín-Terán 1995 et. al.	*Mesoclemmys raniceps*	Unidentified Sapotaceae
Fachín-Terán 1995 et. al.	*Podocnemis unifilis*	*Diospyros sp.*
Fachín-Terán 1995 et. al.	*Podocnemis unifilis*	*Margaritaria sp.*
Fachín-Terán 1995 et. al.	*Podocnemis unifilis*	*Maripa sp.*
Fachín-Terán 1995 et. al.	*Podocnemis unifilis*	*Pouteria sp.*
Fachín-Terán 1995 et. al.	*Podocnemis unifilis*	Unidentified Fabaceae
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Allophylus aldabricus*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Apodytes dimidiata*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Azima tetracantha*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Capparis cartilaginea*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Volkameria glabra*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Cordia subcordata*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Ehretia cymosa*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Ficus sundaica*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Ficus lutea*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Ficus reflexa*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Flacourtia ratmonchii*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Guettarda speciosa*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Aloe aldabrensis*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Cassine aethiopica*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Ochna ciliata*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Pandanus tectorius*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Scaevola taccada*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Solanum aldabrensis*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Terminalia boivinii*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Thespesia populnea*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Thespesia populneides*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Colubrina asiatica*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Pemphis acidula*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Casuarina equisetifolia*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Tournefortia argentata*
Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Abrus prectorius*

Falcón et al. unpubl.	*Aldabrachelys gigantea*	*Acalypha claoxyoides*
Figueroa et. al. 2012	*Podocnemis expansa*	*Erythrina* sp.
Figueroa et. al. 2012	*Podocnemis expansa*	*Ficus* sp.
Figueroa et. al. 2012	*Podocnemis expansa*	*Macrolobium acaciifolium*
Ford and Moll 2004	*Sternotherus odoratus*	*Ludwigia peploides*
Freeman 2010	*Elseya lavarackorum*	*Ficus racemosa*
Freeman 2010	*Elseya lavarackorum*	*Livistona rigida*
Freeman 2010	*Elseya lavarackorum*	*Nauclea orientalis*
Freeman 2010	*Elseya lavarackorum*	*Pandanus aquaticus*
Freeman 2010	*Elseya lavarackorum*	*Passiflora foetida*
Georges and Kennet 1989	*Carettochelys insculpta*	*Ficus racemosa*
Georges and Kennet 1989	*Carettochelys insculpta*	*Pandanus aquaticus*
Georges and Kennet 1989	*Carettochelys insculpta*	*Syzygium forte*
Georges et. al. 2008	*Carettochelys insculpta*	*Artocarpus altilis*
Georges et. al. 2008	*Carettochelys insculpta*	*Canarium indicum*
Georges et. al. 2008	*Carettochelys insculpta*	*Ficus racemosa*
Georges et. al. 2008	*Carettochelys insculpta*	*Nypa* sp.
Georges et. al. 2008	*Carettochelys insculpta*	*Pandanus aquaticus*
Georges et. al. 2008	*Carettochelys insculpta*	*Saccharum robustum*
Georges et. al. 2008	*Carettochelys insculpta*	*Syzygium forte*
Georges et. al. 2008	*Carettochelys insculpta*	*Xylocarpus* sp.
Gibbs et. al. 2008	*Chelonoidis nigra*	*Opuntia megasperma*
Goulding 1980	*Podocnemis expansa*	*Hevea spruceana*
Goulding 1980	*Podocnemis expansa*	*Macrolobium acaciifolium*
Griffiths et. al. 2011	*Aldabrachelys gigantea*	*Diospyros egrettarum*
Gundlach 1880	*Trachemys decussata*	*Annona glabra*
Gundlach 1880	*Trachemys decussata*	*Spondias mombin*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Annona* sp.
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Astrocaryum murumuru*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Casearia macrocarpa*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Cayaponia ophthalmica*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Cecropia membranacea*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Clarisia racemosa*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Combretum* sp.
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Coussapoa* sp.
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Duguetia* sp.
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Ficus* sp.
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Ficus insipida*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Ficus maxima*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Ficus* sp.
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Genipa americana*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Geophila repens*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Guatteria* sp.
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Helicostylis tomentosa*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Inga* sp.
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Iriartea deltoidea*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Jacaratia digitata*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Lecointea amazonica*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Loreya strigosa*

Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Miconia* sp.
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Pourouma cecropiifolia*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Pourouma minor*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Pourouma* sp.
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Pouteria* sp.
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Pseudolmedia laevis*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Quiina peruviana*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Rollinia* sp.
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Salacia gigantea*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Salacia* sp.
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Sorocea* sp.
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Spondias mombin*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Strychnos* sp.
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Tetragastris* sp.
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Virola surinamensis*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Mendoncia bivalvis*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	Unidentified Poaceae 1
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	Unidentified Poaceae 2
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Brosimum lactescens*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Cecropia sciadophylla*
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Ficus* sp1.
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Ficus* sp2.
Hansen et. al. 2008	*Aldabrachelys gigantea*	*Rauvolfia micrantha*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Syzygium mamillatum*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Bulbostylis basalis*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Colubrina asiatica*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Cyperus ligularis*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Dactyloctenium ctenoides*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Eragrostis decumbens*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Eragrostis subaequiglumis*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Euphorbia sp.*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Fimbristylis ferruginea*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Guettarda speciosa*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Lepturus repens*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Ochna ciliata*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Phyllanthus maderaspatensis*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Portulaca mauritiensis*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Scaevola taccada*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Serenoa repens*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Solanum americanum*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Sporobolus testudinum*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Sporobolus virginicus*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Stachytarpheta jamaicensis*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Terminalia boivinii*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Thespesia populnea*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Dactyloctenium pilosum*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Hedyotis prolifera*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Pycreus pumilus*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Ficus sundaica*

Hnatiuk 1978	*Aldabrachelys gigantea*	*Gouania tiliifolia*
Hnatiuk 1978	*Aldabrachelys gigantea*	*Cassine aethiopica*
Iftime and Iftime 2012	*Testudo graeca*	*Nesogenes prostrata*
Iftime and Iftime 2012	*Testudo graeca*	*Cornus mas*
Iftime and Iftime 2012	*Testudo graeca*	*Prunus* sp.
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Pyrus* sp.
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	Unidentified Sapotaceae
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Ananas ananassoides*
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Attalea maripa*
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Brosimum lactescens*
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Castilla ulei*
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Cecropia* sp.
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Celtis* sp.
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Clarisia ilicifolia*
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Eugenia* sp.
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Ficus* sp1.
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Ficus* sp2.
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Genipa americana*
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Geophila cordifolia*
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Guettarda* sp.
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Helicostylis tomentosa*
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Inga* sp.
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Jacaratia spinosa*
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Mouriri* sp.
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Pourouma guianensis*
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Pourouma* sp.
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Pouteria macrophylla*
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Protium* sp.
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Psidium* sp.
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Quiina paraensis*
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Scleria* sp.
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Spondias mombin*
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Tetragastris altissima*
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Xylopia amazonica*
Jerozolimski et. al. 2009	*Chelonoidis denticulata*	Unidentified Myrtaceae
Joshua et. al. 2010	*Chersina angulata*	*Genipa americana*
Kennet and Russel-Smith 1993	*Elseya dentata*	*Nylandtia spinosa*
Kennet and Russel-Smith 1993	*Elseya dentata*	*Ficus racemosa*
Kennet and Russel-Smith 1993	*Elseya dentata*	*Nauclea orientalis*
Kennet and Russel-Smith 1993	*Elseya dentata*	*Pandanus aquaticus*
Kennet and Russel-Smith 1993	*Elseya dentata*	*Syzygium forte*
Kennet and Russel-Smith 1993	*Elseya dentata*	*Terminalia erythrocarpa*
Kennet and Russel-Smith 1993	*Elseya dentata*	*Terminalia microcarpa*
Kennet and Tory 1996	*Elseya dentata*	*Cyclophyllum schultzii*
Kennet and Tory 1996	*Elseya dentata*	*Acacia auriculiformis*
Kennet and Tory 1996	*Elseya dentata*	*Carallia brachiata*
Kennet and Tory 1996	*Elseya dentata*	*Ficus racemosa*
Kennet and Tory 1996	*Elseya dentata*	*Morinda citrifolia*
Kennet and Tory 1996	*Elseya dentata*	*Nauclea orientalis*

Kennet and Tory 1996	*Elseya dentata*	*Pandanus aquaticus*
Kennet and Tory 1996	*Elseya dentata*	*Terminalia erythrocarpa*
Kimmons and Moll 2010	*Chelydra serpentina*	*Ambrosia sp.*
Kimmons and Moll 2010	*Chelydra serpentina*	*Echinochloa crus-galli*
Kimmons and Moll 2010	*Chelydra serpentina*	*Elymus repens*
Kimmons and Moll 2010	*Chelydra serpentina*	*Morus* sp.
Kimmons and Moll 2010	*Chelydra serpentina*	*Panicum* sp.
Kimmons and Moll 2010	*Chelydra serpentina*	*Polygonum* sp.
Kimmons and Moll 2010	*Chelydra serpentina*	*Ranunculus sceleratus*
Kimmons and Moll 2010	*Trachemys scripta*	*Rumex crispus*
Kimmons and Moll 2010	*Trachemys scripta*	*Echinochloa crus-galli*
Kimmons and Moll 2010	*Trachemys scripta*	*Morus* sp.
Kimmons and Moll 2010	*Trachemys scripta*	*Polygonum* sp.
Kimmons and Moll 2010	*Trachemys scripta*	*Ranunculus sceleratus*
Kimmons and Moll 2010	*Trachemys scripta*	*Rumex crispus*
Kimmons and Moll 2010	*Trachemys scripta*	*Rumex obtusifolius*
Kimmons and Moll 2010	*Trachemys scripta*	*Setaria verticillata*
Kimmons and Moll 2010	*Chelydra serpentina*	*Silene nocturna*
Kimmons and Moll 2010	*Chelydra serpentina*	*Echinochloa crus-galli*
Kimmons and Moll 2010	*Chelydra serpentina*	*Morus* sp.
Kimmons and Moll 2010	*Trachemys scripta*	*Rumex crispus*
Kimmons and Moll 2010	*Trachemys scripta*	*Echinochloa crus-galli*
Kimmons and Moll 2010	*Trachemys scripta*	*Morus* sp.
Klimstra and Newsome 1960	*Terrapene carolina*	*Rumex crispus*
Klimstra and Newsome 1960	*Terrapene carolina*	*Hordeum* sp.
Klimstra and Newsome 1960	*Terrapene carolina*	*Bromus* sp.
Klimstra and Newsome 1960	*Terrapene carolina*	*Paspalum* sp.
Klimstra and Newsome 1960	*Terrapene carolina*	*Rubus* sp.
Klimstra and Newsome 1960	*Terrapene carolina*	*Prunus* sp.
Klimstra and Newsome 1960	*Terrapene carolina*	*Fragaria* sp.
Klimstra and Newsome 1960	*Terrapene carolina*	*Diospyros virginiana*
Klimstra and Newsome 1960	*Terrapene carolina*	*Morus rubra*
Klimstra and Newsome 1960	*Terrapene carolina*	*Polygonum* sp.
Klimstra and Newsome 1960	*Terrapene carolina*	Unidentified Caryophillaceae
Klimstra and Newsome 1960	*Terrapene carolina*	*Galium* sp.
Klimstra and Newsome 1960	*Terrapene carolina*	*Ambrosia* sp.
Klimstra and Newsome 1960	*Terrapene carolina*	Unidentified Chenopodiaceae
Klimstra and Newsome 1960	*Terrapene carolina*	Unidentified Cyperaceae
Klimstra and Newsome 1960	*Terrapene carolina*	*Vitis* sp.
Kuchling and Bloxam 1988	*Pyxis planicauda*	*Breonia perrieri*
Kuchling and Bloxam 1988	*Pyxis planicauda*	*Broussonetia greveana*
Lagler 1943	*Chelydra serpentina*	*Nymphaea odorata*
Lagler 1943	*Chelydra serpentina*	*Bidens* sp.
Lagler 1943	*Chrysemys picta*	*Nymphaea odorata*
Lagler 1943	*Chrysemys picta*	*Triticum* sp.
Lagler 1943	*Chrysemys picta*	*Zea mays*
Lagler 1943	*Emys blandingii*	*Cornus amomum*
Lagler 1943	*Emys blandingii*	*Bidens* sp.
Lagler 1943	*Graptemys geographica*	*Potamogeton* sp.

Lagler 1943	*Sternotherus odoratus*	*Cornus amomum*
Lagler 1943	*Sternotherus odoratus*	*Nuphar* sp.
Lagler 1943	*Sternotherus odoratus*	*Nymphaea odorata*
Lagler 1943	*Sternotherus odoratus*	*Bidens* sp.
Lambiris et. al. 1989	*Kinixys spekii*	*Uapaca kirkiana*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Abuta selloana*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Acrocomia aculeata*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Archontophoenix cunninghamiana*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Artocarpus heterophyllus*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Casearia sylvestris*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Cecropia pachystachya*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Clusia criuva*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Cordia ecalyculata*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Cryptocarya mandioccana*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Eriobotrya japonica*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Eugenia uniflora*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Euterpe edulis*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Genipa americana*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Hymenaea courbaril*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Inga* sp.
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Jacaratia spinosa*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Licuala grandis*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Litchi chinensis*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Malpighia* sp.
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Melia azedarach*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Ocotea catharinensis*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Philodendron bipinnatifidum*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Plinia cauliflora*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Psidium cattleianum*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Quiina glaziovii*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Sabal maritima*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Spondias purpurea*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Syagrus oleracea*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Syagrus romanzoffiana*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Syzygium cumini*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Talisia esculenta*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Hyophorbe indica*
LautenschlagerRodrigues 2016	*Chelonoidis carbonaria*	*Cordia africana*
Leuteritz 2003	*Astrochelys radiata*	*Clerodendrum perrieri*
Leuteritz 2003	*Astrochelys radiata*	*Diospyros myriophylla*
Leuteritz 2003	*Astrochelys radiata*	*Operculicarya pachypus*
Leuteritz 2003	*Astrochelys radiata*	*Opuntia sp.*
Leuteritz 2003	*Astrochelys radiata*	*Lycium acutifolium*
Leuteritz 2003	*Astrochelys radiata*	*Sclerocarya birrea*
Leuteritz 2003	*Astrochelys radiata*	*Tetraena madagascariensis*
Limpus and Limpus 2000	*Chelonia mydas*	*Avicennia marina*
Limpus and Limpus 2000	*Chelonia mydas*	*Rhizophora sp.*
Lingard et. al. 2003	*Astrochelys radiata*	*Operculicarya decaryi*
Lingard et. al. 2003	*Astrochelys radiata*	*Opuntia ficus-indica*

Lingard et. al. 2003	*Astrochelys radiata*	*Opuntia monacantha*
Liu et. al. 2004	*Terrapene carolina*	*Annona glabra*
Liu et. al. 2004	*Terrapene carolina*	*Coccoloba uvifera*
Liu et. al. 2004	*Terrapene carolina*	*Coccothrinax argentata*
Liu et. al. 2004	*Terrapene carolina*	*Ficus* sp.
Liu et. al. 2004	*Terrapene carolina*	*Manilkara zapota*
Liu et. al. 2004	*Terrapene carolina*	*Morinda royoc*
Liu et. al. 2004	*Terrapene carolina*	*Mosiera longipes*
Liu et. al. 2004	*Terrapene carolina*	*Paspalum* sp.
Liu et. al. 2004	*Terrapene carolina*	*Smilax havanensis*
Liu et. al. 2004	*Terrapene carolina*	Unidentified Fabaceae
Liu et. al. 2004	*Terrapene carolina*	*Byrsonima lucida*
Liu et. al. 2004	*Terrapene carolina*	*Leucothrinax morrisii*
Liu et. al. 2004	*Terrapene carolina*	*Setaria* sp.
Loehr 2002	*Homopus signatus*	*Antizoma* sp.
Loehr 2002	*Homopus signatus*	*Crassula thunbergiana*
Loehr 2002	*Homopus signatus*	*Grielum humifusum*
Loehr 2002	*Homopus signatus*	*Heliophila variabilis*
Loehr 2002	*Homopus signatus*	*Oxalis* sp.
Macip-Rios et. al. 2010	*Kinosternon integrum*	*Argemone ochroleuca*
Macip-Rios et. al. 2010	*Kinosternon integrum*	*Lemna* sp.
Macip-Rios et. al. 2010	*Kinosternon integrum*	*Psidium* sp.
Macip-Rios et. al. 2010	*Kinosternon integrum*	Unidentified Poaceae
Milton 1992	*Stigmochelys pardalis*	*Amaranthus* sp.
Milton 1992	*Stigmochelys pardalis*	*Aptosimum indivisum*
Milton 1992	*Stigmochelys pardalis*	*Argemone mexicana*
Milton 1992	*Stigmochelys pardalis*	*Aristida* sp.
Milton 1992	*Stigmochelys pardalis*	*Atriplex lindleyi*
Milton 1992	*Stigmochelys pardalis*	*Atriplex semibaccata*
Milton 1992	*Stigmochelys pardalis*	*Chamaesyce inequilatera*
Milton 1992	*Stigmochelys pardalis*	*Chenopodium* sp.
Milton 1992	*Stigmochelys pardalis*	*Chrysocoma ciliata*
Milton 1992	*Stigmochelys pardalis*	*Crassula subaphylla*
Milton 1992	*Stigmochelys pardalis*	*Cuspidia cernua*
Milton 1992	*Stigmochelys pardalis*	*Enneapogon desvauxii*
Milton 1992	*Stigmochelys pardalis*	*Enneapogon scaber*
Milton 1992	*Stigmochelys pardalis*	*Eragrostis obtusa*
Milton 1992	*Stigmochelys pardalis*	*Euphorbia* sp.
Milton 1992	*Stigmochelys pardalis*	*Galenia papulosa*
Milton 1992	*Stigmochelys pardalis*	*Heliophila* sp.
Milton 1992	*Stigmochelys pardalis*	*Hermannia* sp.
Milton 1992	*Stigmochelys pardalis*	*Hypertelis salsoloides*
Milton 1992	*Stigmochelys pardalis*	*Lepidium* sp.
Milton 1992	*Stigmochelys pardalis*	*Lessertia annularis*
Milton 1992	*Stigmochelys pardalis*	*Leysera tenella*
Milton 1992	*Stigmochelys pardalis*	*Limeum aethiopicum*
Milton 1992	*Stigmochelys pardalis*	*Lolium* sp.
Milton 1992	*Stigmochelys pardalis*	*Lotononis* sp.
Milton 1992	*Stigmochelys pardalis*	*Malva parviflora*

Milton 1992	*Stigmochelys pardalis*	*Medicago polymorpha*
Milton 1992	*Stigmochelys pardalis*	*Nemesia* sp.
Milton 1992	*Stigmochelys pardalis*	*Osteospermum calendulaceum*
Milton 1992	*Stigmochelys pardalis*	*Pleiospilos compactus*
Milton 1992	*Stigmochelys pardalis*	*Polygonum* sp.
Milton 1992	*Stigmochelys pardalis*	*Sida hederifolia*
Milton 1992	*Stigmochelys pardalis*	*Tetragonia echinata*
Milton 1992	*Stigmochelys pardalis*	*Tetragonia spicata*
Milton 1992	*Stigmochelys pardalis*	*Thesium lineatum*
Milton 1992	*Stigmochelys pardalis*	*Tragus sp.*
Milton 1992	*Stigmochelys pardalis*	*Trianthema triquetra*
Milton 1992	*Stigmochelys pardalis*	*Tribulus terrestris*
Milton 1992	*Stigmochelys pardalis*	*Walafrida* sp.
Milton 1992	*Stigmochelys pardalis*	*Eriocephalus* sp.
Milton 1992	*Stigmochelys pardalis*	*Ursinia* sp.
Milton 1992	*Stigmochelys pardalis*	*Tribolium purpureum*
Milton 1992	*Stigmochelys pardalis*	Unidentified Cyperaceae
Moldowan et. al. 2016	*Chelydra serpentina*	*Nuphar variegata*
Moll 1976	*Graptemys ouachitensis*	*Ulmus americana*
Moll 1989	*Dermatemys mawii*	*Ficus* sp.
Moll 1989	*Dermatemys mawii*	*Ficus obtusiuscula*
Moll and Jansen 1995	*Rhinoclemmys annulata*	*Astrocaryum alatum*
Moll and Jansen 1995	*Rhinoclemmys annulata*	*Faramea suerrensis*
Moll and Jansen 1995	*Rhinoclemmys annulata*	*Jacaratia dolichaula*
Moll and Jansen 1995	*Rhinoclemmys annulata*	*Solanum siparunoides*
Moll and Jansen 1995	*Rhinoclemmys funerea*	*Artocarpus altilis*
Moll and Jansen 1995	*Rhinoclemmys funerea*	*Eichhornia crassipes*
Moll and Jansen 1995	*Rhinoclemmys funerea*	*Ficus* sp.
Moll and Jansen 1995	*Rhinoclemmys funerea*	*Miconia* sp.
Moll and Jansen 1995	*Rhinoclemmys funerea*	*Passiflora foetida*
Moll and Jansen 1995	*Rhinoclemmys annulata*	*Faramea suerrensis*
Moll and Jansen 1995	*Rhinoclemmys annulata*	*Ficus* sp.
Moll and Jansen 1995	*Rhinoclemmys annulata*	*Jacaratia dolichaula*
Moll and Jansen 1995	*Rhinoclemmys annulata*	*Miconia affinis*
Moll and Jansen 1995	*Rhinoclemmys annulata*	*Sonneratia* sp.
Moll and Jansen 1995	*Rhinoclemmys funerea*	*Cecropia* sp.
Moll and Jansen 1995	*Rhinoclemmys funerea*	*Dieffenbachia longispatha*
Moll and Jansen 1995	*Rhinoclemmys funerea*	*Ficus insipida*
Moll and Jansen 1995	*Rhinoclemmys funerea*	*Ipomoea trifida*
Moll and Jansen 1995	*Rhinoclemmys funerea*	*Solanum pimpinellifolium*
Moll and Jansen 1995	*Rhinoclemmys funerea*	*Spondias mombin*
Moolna 2007	*Aldabrachelys gigantea*	*Diospyros egrettarum*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Annona* sp1.
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Annona* sp2.
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Bagassa guianensis*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Duguetia surinamensis*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Ecclinusa guianensis*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Ficus* sp.
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Genipa americana*

Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Geophila repens*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Guettarda argentea*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Mauritia flexuosa*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Myriaspora egensis*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Passiflora* sp.
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Philodendron* sp.
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Spondias mombin*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Trattinnickia ravifolia*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Anacardium giganteum*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Bagassa guianensis*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Bromelia* sp.
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Brosimum potabile*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Clavija* sp.
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Desmoncus polyacanthos*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Duguetia surinamensis*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Duroia eriopila*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Ficus* sp.
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Guettarda argentea*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Licania kunthiana*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Mauritia flexuosa*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Myriaspora egensis*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Passiflora coccinea*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Passiflora vespertilio*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Philodendron* sp.
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Posoqueria* sp.
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Pouteria* sp.
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Pradosia* sp.
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Spondias mombin*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Richardela* sp.
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	*Ecclinusa guianensis*
Moskovits and Bjorndal 1990	*Chelonoidis carbonaria*	Unidentified Lecythidaceae
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Annona* sp1.
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Annona* sp2.
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Bagassa guianensis*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Duguetia surinamensis*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Ecclinusa guianensis*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Ficus* sp.
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Genipa americana*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Geophila repens*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Guettarda argentea*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Mauritia flexuosa*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Myriaspora egensis*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Passiflora* sp.
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Philodendron* sp.
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Spondias mombin*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Trattinnickia* sp.
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Anacardium giganteum*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Bagassa guianensis*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Bromelia* sp.

Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Brosimum potabile*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Clavija* sp.
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Desmoncus polyacanthos*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Duguetia surinamensis*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Duroia eriopila*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Ficus* sp.
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Guettarda argentea*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Licania kunthiana*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Mauritia flexuosa*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Myriaspora egensis*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Passiflora coccinea*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Passiflora vespertilio*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Philodendron* sp.
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Posoqueria* sp.
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Pouteria* sp.
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Pradosia* sp.
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Spondias mombin*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Richardella* sp.
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	*Ecclinusa guianensis*
Moskovits and Bjorndal 1990	*Chelonoidis denticulata*	Unidentified Lecythidaceae
Murray and Wolf 2013	*Gopherus agassizii*	*Opuntia* sp.
Padgett et. al. 2012	*Chrysemys picta*	*Carex* sp.
Padgett et. al. 2012	*Chrysemys picta*	*Decodon verticillatus*
Padgett et. al. 2012	*Chrysemys picta*	*Najas flexilis*
Padgett et. al. 2012	*Chrysemys picta*	*Nuphar variegata*
Padgett et. al. 2012	*Chrysemys picta*	*Nymphaea odorata*
Padgett et. al. 2012	*Chrysemys picta*	*Potamogeton* sp.
Padgett et. al. 2012	*Chrysemys picta*	*Bidens* sp.
Padgett et. al. 2012	*Chrysemys picta*	Unidentified Poaceae
Pemberton and Gilchrist 2009	*Aldabrachelys gigantea*	*Artocarpus altilis*
Pemberton and Gilchrist 2009	*Aldabrachelys gigantea*	*Xylocarpus moluccensis*
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	*Annona glabra*
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	*Combretum laxum*
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	*Eperua purpurea*
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	*Hevea benthamiana*
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	*Leopoldinia piassaba*
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	*Leopoldinia pulchra*
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	*Macrolobium multijugum*
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	*Macrolobium* sp.
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	*Maripa paniculata*
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	*Mauritia flexuosa*
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	*Mauritiella aculeata*
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	*Parahancornia negroensis*
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	*Parinari campestris*
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	*Rauvolfia polyphylla*
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	*Swartzia sericea*
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	*Compsiandra comosa*
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	*Macrolobium angustifolium*
Perez-Eman and Paolillo 1997	*Peltocephalus dumerilianus*	Unidentified Lauraceae

Platt et. al. 2009	*Terrapene carolina bauri*	*Annona glabra*
Platt et. al. 2009	*Terrapene carolina bauri*	*Byrsonima lucida*
Platt et. al. 2009	*Terrapene carolina bauri*	*Coccoloba uvifera*
Platt et. al. 2009	*Terrapene carolina bauri*	*Coccothrinax argentata*
Platt et. al. 2009	*Terrapene carolina bauri*	*Ficus* sp.
Platt et. al. 2009	*Terrapene carolina bauri*	*Morinda royoc*
Platt et. al. 2009	*Terrapene carolina bauri*	*Mosiera longipes*
Platt et. al. 2009	*Terrapene carolina bauri*	*Socratea exorrhiza*
Platt et. al. 2009	*Terrapene carolina bauri*	*Leucothrinax morrisii*
Platt et. al. 2009	*Terrapene carolina bauri*	Unidentified Fabaceae
Platt et. al. 2010	*Heosemys depressa*	*Ficus hispida*
Platt et. al. 2010	*Heosemys depressa*	Erythrina suberosa
Platt et. al. 2010	*Heosemys depressa*	*Grewia nervosa*
Platt et. al. 2014a	*Vijayachelys silvatica*	*Dillenia pentagyna*
Platt et. al. 2014a	*Vijayachelys silvatica*	*Salacca* sp.
Platt et. al. 2014b	*Heosemys depressa*	*Dillenia pentagyna*
Platt et. al. 2016	*Kinosternon hirtipes*	*Paspalum distichum*
Platt et. al. 2016	*Kinosternon hirtipes*	*Prosopis glandulosa*
Plummer and Farrar 1981	*Apalone mutica*	*Morus* sp.
Plummer and Farrar 1981	*Apalone mutica*	*Populus deltoides*
Plummer and Farrar 1981	*Apalone mutica*	*Morus* sp.
Plummer and Farrar 1981	*Apalone mutica*	*Populus* sp.
Raney and Rachner 194 2	*Chrysemys picta*	*Nuphar variegata*
Rasoma et. al. 2013	*Astrochelys radiata*	*Gyrocarpus americanus*
Rasoma et. al. 2013	*Astrochelys radiata*	*Paederia grandidieri*
Rasoma et. al. 2013	*Astrochelys radiata*	*Radamaea montana*
Rasoma et. al. 2013	*Astrochelys radiata*	*Salvadora angustifolia*
Rasoma et. al. 2013	*Astrochelys radiata*	*Olax dissitiflora*
Renvoize 1971	*Aldabrachelys gigantea*	*Pandanus tectorius*
Rick and Bowman 1961	*Chelonoidis porteri*	*Solanum siparunoides*
Rouag et. al. 2008	*Testudo graeca*	*Anagallis minima*
Rouag et. al. 2008	*Testudo graeca*	*Linaria pinifolia*
Rouag et. al. 2008	*Testudo graeca*	*Tuberaria guttata*
Rouag et. al. 2008	*Testudo graeca*	*Coronilla scorpioides*
Rust and Roth 1981	*Terrapene carolina*	*Podophyllum peltatum*
Santos-Júnior 2009	*Podocnemis erythrocephala*	*Pouteria* sp.
Santos-Júnior 2009	*Podocnemis erythrocephala*	*Posoqueria* sp.
Santos-Júnior 2009	*Podocnemis erythrocephala*	*Smilax coriacea*
Santos-Júnior 2009	*Podocnemis erythrocephala*	Unidentified Fabaceae
Santos-Júnior 2009	*Podocnemis erythrocephala*	Unidentified Poaceae
Setlalekgomo and Sesiny 2014	*Psammobates oculifer*	*Grewia flavescens*
Setlalekgomo and Sesinyi 2014	*Psammobates oculifer*	Unidentified
Snider 1993	*Gopherus agassizii*	*Opuntia engelmannii*
Stone and Moll 2006	*Terrapene carolina*	*Fragaria* sp.
Stone and Moll 2006	*Terrapene carolina*	*Podophyllum peltatum*
Stone and Moll 2006	*Terrapene carolina*	*Rubus allegheniensis*
Stone and Moll 2006	*Terrapene ornata*	*Fragaria* sp.
Stone and Moll 2006	*Terrapene ornata*	*Podophyllum peltatum*
Stone and Moll 2006	*Terrapene ornata*	*Rubus allegheniensis*

Stone and Moll 2009	*Terrapene carolina*	*Ambrosia artemisiifolia*
Stone and Moll 2009	*Terrapene carolina*	*Celtis* sp.
Stone and Moll 2009	*Terrapene carolina*	*Cornus* sp.
Stone and Moll 2009	*Terrapene carolina*	*Fragaria virginiana*
Stone and Moll 2009	*Terrapene carolina*	*Morus* sp.
Stone and Moll 2009	*Terrapene carolina*	*Passiflora* sp.
Stone and Moll 2009	*Terrapene carolina*	*Phytolacca americana*
Stone and Moll 2009	*Terrapene carolina*	*Platanus occidentalis*
Stone and Moll 2009	*Terrapene carolina*	*Podophyllum peltatum*
Stone and Moll 2009	*Terrapene carolina*	*Rubus* sp.
Stone and Moll 2009	*Terrapene carolina*	*Vaccinium* sp.
Stone and Moll 2009	*Terrapene carolina*	*Vitis* sp.
Stone and Moll 2009	*Terrapene carolina*	Unidentified Polygonaceae
Stone and Moll 2009	*Terrapene carolina*	Unidentified
Stone and Moll 2009	*Terrapene ornata*	*Fragaria virginiana*
Stone and Moll 2009	*Terrapene ornata*	*Galium* sp.
Stone and Moll 2009	*Terrapene ornata*	*Morus* sp.
Stone and Moll 2009	*Terrapene ornata*	*Prunus* sp.
Stone and Moll 2009	*Terrapene ornata*	*Rubus* sp.
Stone and Moll 2009	*Terrapene ornata*	Unidentified Polygonaceae
Stone and Moll 2009	*Terrapene ornata*	Unidentified Poaceae
Stone and Moll 2009	*Terrapene ornata*	Unidentified Cyperaceae
Strong and Fragoso 2006	*Chelonoidis carbonaria*	*Aechmea* sp.
Strong and Fragoso 2006	*Chelonoidis carbonaria*	*Ficus* sp.
Strong and Fragoso 2006	*Chelonoidis carbonaria*	*Genipa americana*
Strong and Fragoso 2006	*Chelonoidis denticulata*	*Aechmea* sp.
Strong and Fragoso 2006	*Chelonoidis denticulata*	*Ficus* sp.
Strong and Fragoso 2006	*Chelonoidis denticulata*	*Genipa americana*
Sung et. al. 2016	*Platysternon megacephalum*	*Ficus* sp.
Sung et. al. 2016	*Platysternon megacephalum*	*Machilus breviflora*
Sung et. al. 2016	*Platysternon megacephalum*	*Machilus thunbergii*
Sung et. al. 2016	*Platysternon megacephalum*	*Turpinia arguta*
Teran et. al. 1995	*Phrynops geoffroanus*	*Diospyros* sp.
Teran et. al. 1995	*Phrynops geoffroanus*	*Margaritaria nobilis*
Teran et. al. 1995	*Phrynops geoffroanus*	*Maripa sp.*
Teran et. al. 1995	*Phrynops geoffroanus*	*Pouteria sp.*
Teran et. al. 1995	*Phrynops geoffroanus*	Unidentified Fabaceae
Tol et. al. 2017	*Chelonia mydas*	*Halodule uninervis*
Tol et. al. 2017	*Chelonia mydas*	*Halophila decipiens*
Tol et. al. 2017	*Chelonia mydas*	*Zostera muelleri*
Tulipani and Lipcius 2014	*Malaclemys terrapin*	*Zostera marina*
Turner et. al. 1984	*Gopherus agassizii*	*Opuntia* sp.
van Dijk 1998	*Indotestudo elongata*	*Cyanotis cristata*
van Dijk 1998	*Indotestudo elongata*	*Dillenia* sp.
van Dijk 1998	*Indotestudo elongata*	*Ficus racemosa*
van Dijk 1998	*Indotestudo elongata*	*Olax scandens*
Varela and Bucher 2002	*Chelonoidis chilensis*	*Celtis pallida*
Varela and Bucher 2002	*Chelonoidis chilensis*	*Prosopis elata*
Varela and Bucher 2002	*Chelonoidis chilensis*	*Prosopis nigra*

Varela and Bucher 2002	*Chelonoidis chilensis*	*Prosopis torquata*
Varela and Bucher 2002	*Chelonoidis chilensis*	*Ziziphus mistol*
Varela and Bucher 2002	*Chelonoidis chilensis*	*Celtis pallida*
Varela and Bucher 2002	*Chelonoidis chilensis*	*Ziziphus mistol*
Veerappan and Vasudevan 2012	*Indotestudo travancorica*	*Dillenia pentagyna*
Vijaya 1982	*Indotestudo forsteni*	*Artocarpus heterophyllus*
Vijaya 1982	*Vijayachelys silvatica*	*Artocarpus heterophyllus*
Vijaya 1982	*Vijayachelys silvatica*	*Dillenia pentagyna*
Vijaya 1982	*Vijayachelys silvatica*	*Cordia peruviana*
Vijaya 1983	*Indotestudo travancorica*	*Artocarpus heterophyllus*
Vijaya 1983	*Indotestudo travancorica*	*Dillenia pentagyna*
Vogt and Guzmán 1988	*Kinosternon leucostomum*	*Ficus* sp.
Vogt and Guzmán 1988	*Kinosternon leucostomum*	*Piper* sp.
Vogt and Guzmán 1988	*Kinosternon leucostomum*	*Pulcheni armata*
Vogt and Guzmán 1988	*Staurotypus triporcatus*	*Diospyros nigra*
Vogt et. al. 2009	*Rhinoclemmys aerolata*	*Byrsonima crassifolia*
Vogt et. al. 2009	*Rhinoclemmys aerolata*	*Eugenia* sp.
Vogt et. al. 2009	*Rhinoclemmys aerolata*	*Miconia* sp.
Waibel et. al. 2012	*Aldabrachelys gigantea*	*Lantana camara*
Waibel et. al. 2012	*Aldabrachelys gigantea*	*Mimusops coriacea*
Waibel et. al. 2012	*Aldabrachelys gigantea*	*Wikstroemia indica*
Waibel et. al. 2012	*Aldabrachelys gigantea*	*Adonidia merrillii*
Waller at. al. 1989	*Chelonoidis chilensis*	*Goldmanceggea glauca*
Waller et. al. 1989	*Chelonoidis chilensis*	*Cereus aethiops*
Waller et. al. 1989	*Chelonoidis chilensis*	*Daucus pusillus*
Waller et. al. 1989	*Chelonoidis chilensis*	*Geoffroea decorticans*
Waller et. al. 1989	*Chelonoidis chilensis*	*Monttea aphylla*
Waller et. al. 1989	*Chelonoidis chilensis*	*Plantago patagonica*
Waller et. al. 1989	*Chelonoidis chilensis*	*Prosopis alpataco*
Waller et. al. 1989	*Chelonoidis chilensis*	*Schismus barbatus*
Wang et. al. 2011	*Chelonoidis carbonaria*	*Acrocomia aculeata*
Wang et. al. 2011	*Chelonoidis carbonaria*	*Agonandra brasiliensis*
Wang et. al. 2011	*Chelonoidis carbonaria*	*Annona cornifolia*
Wang et. al. 2011	*Chelonoidis carbonaria*	*Annona dioica*
Wang et. al. 2011	*Chelonoidis carbonaria*	*Ficus* sp.
Wang et. al. 2011	*Chelonoidis carbonaria*	*Genipa americana*
Wang et. al. 2011	*Chelonoidis carbonaria*	*Hancornia speciosa*
Wang et. al. 2011	*Chelonoidis carbonaria*	*Mouriri elliptica*
Wang et. al. 2011	*Chelonoidis carbonaria*	*Pouteria gardneri*
Wang et. al. 2011	*Chelonoidis carbonaria*	*Protium heptaphyllum*
Wang et. al. 2011	*Chelonoidis carbonaria*	*Psidium nutans*
Wang et. al. 2011	*Chelonoidis carbonaria*	*Psidium guajava*
Wang et. al. 2011	*Chelonoidis carbonaria*	*Syagrus flexuosa*
Wang et. al. 2011	*Chelonoidis carbonaria*	*Syzygium cumini*
Wang et. al. 2011	*Chelonoidis carbonaria*	*Vitex cymosa*
Wang et. al. 2011	*Chelonoidis carbonaria*	*Cordiera sessilis*
Wang et. al. 2011	*Chelonoidis carbonaria*	*Byrsonima cydoniifolia*
Whitaker 2009	*Vijayachelys silvatica*	*Ficus pertusa*
Wilson and Lawler 2008	*Emydura macquarii krefftii*	*Ficus* sp.

Appendix 3: Studies from which data on the gut retention times (GRT) of chelonians were extracted, and chelonian mean GRT and mass. '*NA*' indicates that the mean GRT was not available (only the range; see Fig. 6).

Reference	Chelonian species	Mean GRT (d)	Mass (kg)
Amorocho & Reina 2008	*Chelonia mydas*	23.7	160.0
Andriantsaralaza et al. 2013	*Aldabrachelys gigantea*	*NA*	117.2
Barboza 1995	*Gopherus agassizii*	10.8	2.8
Bjorndal 1987	*Gopherus polyphemus*	13.0	4.1
Bjorndal 1989	*Chelonoidis carbonaria*	2.6	2.0
Bjorndal 1989	*Chelonoidis denticulata*	3.6	2.0
Bjorndal 1990	*Pseudemys nelsoni*	2.8	3.8
Bjorndal and Bolten 1993	*Pseudemys nelsoni*	3.1	3.8
Bjorndal and Bolten 1993	*Trachemys scripta*	4.9	1.9
Blake et al. 2012	*Chelonoidis nigra*	12.0	175.0
Braun & Brooks 1987	*Terrapene carolina*	*NA*	0.4
Davenport et al. 1992	*Batagur baska*	*NA*	17.9
Elbers 2010	*Macrochelys temminckii*	*NA*	78.9
Falcón et al. unpubl.	*Aldabrachelys gigantea*	15.0	117.2
Franz et al. 2011	*Aldabrachelys gigantea*	6.8	117.2
Franz et al. 2011	*Centrochelys sulcata*	15.9	43.0
Franz et al. 2011	*Chelonoidis nigra*	8.6	175.0
Franz et al. 2011	*Testudo graeca*	6.8	1.4
Franz et al. 2011	*Testudo hermanni*	5.0	1.3
Guzmán & Stevenson 2008	*Chelonoidis denticulata*	21.0	2.0
Hailey 1997	*Kinixys spekii*	5.6	0.6
Hailey 1997	*Stigmochelys pardalis*	5.2	20.0
Hailey 1998	*Kinixys spekii*	5.5	0.6
Hamilton and Coe 1982	*Aldabrachelys gigantea*	12.2	117.2
Hansen et al. 2008	*Aldabrachelys gigantea*	14.0	117.2
Hatt et al. 2002	*Chelonoidis nigra*	10.2	175.0
Jansen & Moll 1995	*Rhinoclemmys annulata*	1.5	1.4
Jansen & Moll 1995	*Rhinoclemmys funerea*	1.8	0.9
Jerozolimski et al. 2009	*Chelonoidis denticulata*	8.3	2.0
Kimmons & Moll 2010	*Chelydra serpentina*	2.0	5.2
Kimmons & Moll 2010	*Chelydra serpentina*	2.0	5.2
Kimmons & Moll 2010	*Chelydra serpentina*	2.3	5.2
Kimmons & Moll 2010	*Trachemys scripta*	2.8	1.9
Kimmons & Moll 2010	*Trachemys scripta*	2.9	1.9
Kimmons & Moll 2010	*Trachemys scripta*	3.7	1.9
Lautenschlager Rodrigues 2016	*Chelonoidis carbonaria*	6.9	2.0
Legler & Vogt 2013	*Rhinoclemmys aereolata*	3.0	0.7
Lickel 2010	*Stigmochelys pardalis*	15.8	20.0
Meienberger et al. 1993	*Gopherus agassizii*	21.5	2.8
Parmenter 1981	*Chelydra serpentina*	1.3	5.2
Parmenter 1981	*Chrysemys picta*	2.5	0.4
Parmenter 1981	*Chrysemys scripta*	2.5	0.4
Parmenter 1981	*Sternotherus minor*	2.4	0.2
Parmenter 1981	*Sternotherus odoratus*	2.0	0.1

Rick & Bowman 1961	*Chelonoidis porteri*	*NA*	175.0
Sadeghayobi et al. 2011	*Chelonoidis nigra*	10.1	175.0
Setlalekgomo & Sesiny 2014	*Psammobates oculifer*	NA	0.3
Setlalekgomo and Sesinyi 2014	*Psammobates oculifer*	4.0	0.3
Stone & Moll 2006	*Terrapene carolina*	*NA*	0.4
Stone & Moll 2006	*Terrapene ornata*	*NA*	0.4
Tracy et al. 2006	*Gopherus agassizii*	9.5	2.8
Valente et al. 2008	*Caretta caretta*	11.5	109.2
Varela & Bucher 2002	*Chelonoidis chilensis*	8.0	3.2
Waibel et al. 2012	*Aldabrachelys gigantea*	15.5	117.2

Appendix 4: Studies from which data on the home range size of chelonians were extracted, and chelonian mean home range and mass. See Figure 7a for ranges (minimum and maximum home range size).

Reference	Chelonian species	Home range (ha)	Mass (kg)
Barret 1990	*Gopherus agassizii*	19.0	2.8
Baxter 2015	*Aldabrachelys gigantea*	10.5	117.2
Bernstein et al. 2007	*Terrapene ornata*	5.8	0.4
Bridget and Echternacht 2009	*Terrapene carolina*	2.3	0.4
Carter et al. 1999	*Clemmys muhlenbergii*	0.5	0.2
Chase et al. 1989	*Clemmys muhlenbergii*	0.1	0.2
Diemer 1992	*Gopherus polyphemus*	0.9	4.1
Doroff and Keith 1990	*Terrapene ornata*	8.7	0.4
Duda et al. 1999	*Gopherus agassizii*	12.5	2.8
Edge et al. 2015	*Emydoidea blandingii*	59.2	1.2
Eubanks et al. 2003	*Gopherus polyphemus*	0.8	4.1
Forero-Medina et al. 2012	*Mesoclemmys dahli*	15.3	0.8
Franks et al. 2011	*Gopherus agassizii*	7.3	2.8
Galois et al. 2002	*Apalone spinifera*	24.2	4.8
Geffen and Mendelssohn 1988	*Testudo kleinmanni*	26.4	0.4
Hailey and Coulson 1996	*Kinixys spekii*	1.9	0.6
Hailey and Coulson 1996	*Stigmochelys pardalis*	26.0	20.0
Innes et al. 2008	*Emydoidea blandingii*	4.9	1.2
Jones 1996	*Graptemys flavimaculata*	3.5	0.9
Judd and Rose 1983	*Gopherus berlandieri*	0.4	1.8
Lawson 2006	*Kinixys erosa*	14.2	1.1
Lawson 2006	*Kinixys homeana*	20.0	1.1
Litzgus and Mousseau 2004	*Clemmys guttata*	7.5	0.2
Lue and Chen 1999	*Cuora flavomarginata*	1.1	0.5
Mazzotti et al. 2002	*Testudo hermanni*	6.0	1.3
McMaster and Downs 2009	*Stigmochelys pardalis*	122.4	20.0
Millar and Blouin-Demers 2011	*Emydoidea blandingii*	12.0	1.2
Morrow et al. 2001	*Clemmys muhlenbergii*	0.6	0.2
Moskovits and Kiester 1987	*Chelonoidis carbonaria*	26.3	2.0
Moskovits and Kiester 1987	*Chelonoidis denticulata*	36.1	2.0
Nieuwot 1996	*Terrapene ornata*	1.6	0.4
O'connor et al. 1994	*Gopherus agassizii*	27.3	2.8
Obbard and Brooks 1981	*Chelydra serpentina*	3.5	5.2
Roe and Arthur 2008	*Chelodina longicolis*	11.5	1.3
Ross and Anderson 1990	*Emydoidea blandingii*	0.6	1.2
Rowe 2003	*Chrysemys picta*	1.2	0.4
Rowe and Moll 1991	*Emydoidea blandingii*	84.5	1.2
Seminoff et al. 2002	*Chelonia mydas*	1662.0	160.0
Smith and Cherry 2016	*Glyptemys muhlenbergii*	0.8	0.1
Stickel 1989	*Terrapene carolina*	1.2	0.4
Strang 1983	*Clemmys insculpta*	0.0	0.2
Strang 1983	*Terrapene carolina*	0.0	0.4

Appendix 5: Studies from which data on the displacement distances of chelonians were extracted, and chelonian mean displacement distance and mass. '*NA*' indicates that the mean displacement distance was not available (only the range; see Fig. 7b).

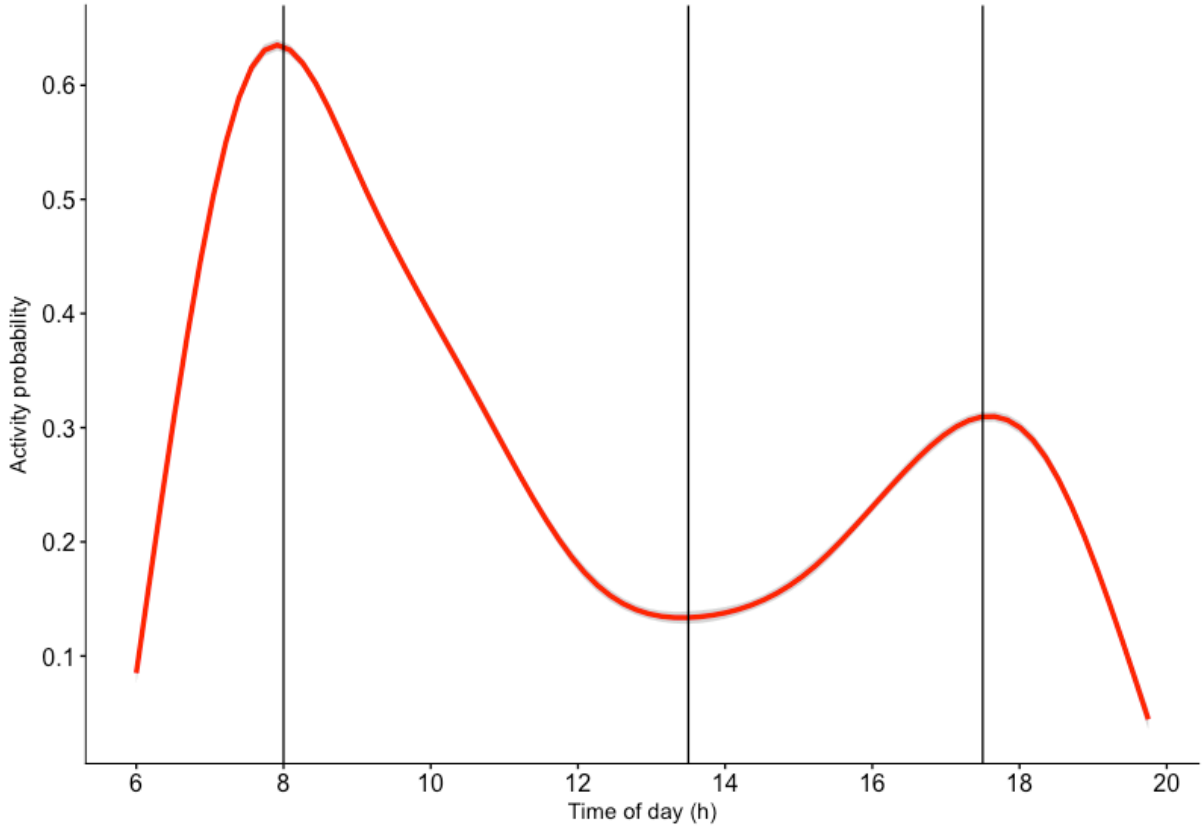
Reference	Chelonian species	Displacement (m d^{-1})	Mass (kg)
Baxter 2015	*Aldabrachelys gigantea*	191.8	117.2
Birkhead et al. 2005	*Gopherus polyphemus*	*NA*	4.1
Brown and Brooks 1993	*Chelydra serpentina*	300.5	5.2
DÍaz-Paniagua	*Testudo graeca*	50.0	1.4
Duda et al. 1999	*Gopherus agassizii*	41.7	2.8
Geffen and Mendelssohn 1988	*Testudo kleinmanni*	26.0	0.4
Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*NA*	2.0
Hailey 1989	*Testudo hermanni*	78.0	1.3
Hailey and Coulson 1996	*Kinixys spekii*	172.0	0.6
Hailey and Coulson 1996	*Stigmochelys pardalis*	435.0	20.0
Innes et al. 2008	*Emydoidea blandingii*	30.9	1.2
Kimmons & Moll 2010	*Trachemys scripta*	*NA*	1.9
Kimmons & Moll 2010	*Chelydra serpentina*	*NA*	5.2
Lambiris et al. 1989	*Kinixys spekii*	*NA*	0.6
Mazzotti et al. 2002	*Testudo hermanni*	55.9	1.3
Millar and Blouin-Demers 2011	*Emydoidea blandingii*	214.8	1.2
Moll & Jansen 1995	*Rhinoclemmys funerea*	*NA*	0.9
Moll & Jansen 1995	*Rhinoclemmys annulata*	*NA*	1.4
Morrow et al. 2001	*Clemmys muhlenbergii*	3.3	0.2
Moskovits and Kiester 1987	*Chelonoidis carbonaria*	0.4	2.0
Moskovits and Kiester 1987	*Chelonoidis denticulata*	0.5	2.0
Nieuwot 1996	*Terrapene ornata*	13.4	0.4
Ross and Anderson 1990	*Emydoidea blandingii*	71.4	1.2
Rowe 2003	*Chrysemys picta*	250.8	0.4
Rowe and Moll 1991	*Emydoidea blandingii*	40.4	1.2
Smith and Cherry 2016	*Glyptemys muhlenbergii*	14.1	0.1
Strang 1983	*Clemmys insculpta*	108.0	0.2
Strang 1983	*Terrapene carolina*	40.0	0.4
Travis et al. 2014	*Chelydra serpentina*	147.5	5.2

Appendix 6: Studies from which data on the effect of chelonian gut passage on germination were extracted. References for Table 2 in the main text.

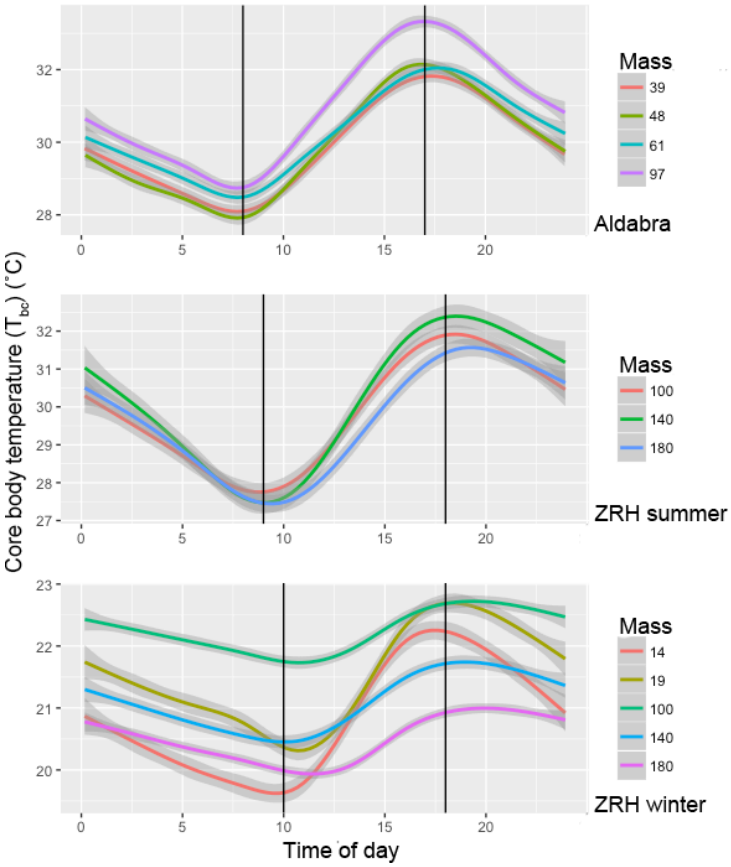
Reference no.	Reference	Chelonian species	Plant species
[1]	Waibel et. al. 2012	*Aldabrachelys gigantea*	*Adonidia merrillii*
[2]	Griffiths et. al. 2011	*Aldabrachelys gigantea*	*Diospyros egrettarum*
[3]	Moolna 2008	*Aldabrachelys gigantea*	*Diospyros egrettarum*
[4]	Andriantsaralaza et. al. 2013	*Aldabrachelys gigantea*	*Adansonia fony*
[5]	Hansen et. al. 2008	*Aldabrachelys gigantea*	*Syzygium mamillatum*
[1]	Waibel et. al. 2012	*Aldabrachelys gigantea*	*Mimusops coriacea*
[1]	Waibel et. al. 2012	*Aldabrachelys gigantea*	*Wikstroemia indica*
[1]	Waibel et. al. 2012	*Aldabrachelys gigantea*	*Lantana camara*
[6]	Varela and Bucher 2002	*Chelonoidis chilensis*	*Celtis pallida*
[6]	Varela and Bucher 2002	*Chelonoidis chilensis*	*Ziziphus mistol*
[7]	Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Rauvolfia micrantha*
[7]	Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Brosimum lactescens*
[7]	Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Ficus* sp1.
[7]	Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Ficus* sp2.
[8]	Jerozolimski et. al. 2009	*Chelonoidis denticulata*	*Genipa americana*
[7]	Guzmán and Stevenson 2008	*Chelonoidis denticulata*	*Cecropia sciadophylla*
[9]	Blake et. al. 2012	*Chelonoidis nigra*	*Opuntia echios*
[9]	Blake et. al. 2012	*Chelonoidis nigra*	*Hippomane mancinella*
[9]	Blake et. al. 2012	*Chelonoidis nigra*	*Psidium galapageium*
[9]	Blake et. al. 2012	*Chelonoidis nigra*	*Psidium guajava*
[9]	Blake et. al. 2012	*Chelonoidis nigra*	*Passiflora edulis*
[10]	Rick and Bowman 1961	*Chelonoidis porteri*	*Solanum siparunoides*
[11]	Kimmons and Moll 2010	*Chelydra serpentina*	*Morus sp.*
[11]	Kimmons and Moll 2010	*Chelydra serpentina*	*Echinochloa crus-galli*
[11]	Kimmons and Moll 2010	*Chelydra serpentina*	*Rumex crispus*
[12]	Calvino-Cancela et. al. 2007	*Emys orbicularis*	*Nymphaea alba*
[13]	Carlson et. al. 2003	*Gopherus polyphemus*	*Paspalum setaceum*
[14]	Elbers and Moll 2011	*Macrochelys temminckii*	*Nyssa aquatica*
[14]	Elbers and Moll 2011	*Macrochelys temminckii*	*Diospyros virginiana*
[14]	Elbers and Moll 2011	*Macrochelys temminckii*	*Quercus phellos*
[15]	Sung et. al. 2016	*Platysternon megacephalum*	*Machilus sp.*
[16]	Setlalekgomo and Sesinyi 2014	*Psammobates oculifer*	*Grewia flavescens*
[17]	Moll and Jansen 1995	*Rhinoclemmys annulata*	*Jacaratia dolichaula*
[17]	Moll and Jansen 1995	*Rhinoclemmys annulata*	*Faramea suerrensis*
[17]	Moll and Jansen 1995	*Rhinoclemmys funerea*	*Solanum pimpinellifolium*
[18]	Braun and Brooks 1987	*Terrapene carolina*	*Arisaema triphyllum*
[19]	Liu et. al. 2004	*Terrapene carolina*	*Thrinax morrisii*
[18]	Braun and Brooks 1987	*Terrapene carolina*	*Podophyllum peltatum*
[20]	Rust and Roth 1981	*Terrapene carolina*	*Podophyllum peltatum*
[18]	Braun and Brooks 1987	*Terrapene carolina*	*Gaylussacia baccata*
[18]	Braun and Brooks 1987	*Terrapene carolina*	*Vaccinium vacillans*
[19]	Liu et. al. 2004	*Terrapene carolina*	*Byrsonima lucida*
[18]	Braun and Brooks 1987	*Terrapene carolina*	*Morus alba*
[18]	Braun and Brooks 1987	*Terrapene carolina*	*Phytolacca americana*
[19]	Liu et. al. 2004	*Terrapene carolina*	*Serenoa rapens*
[18]	Braun and Brooks 1987	*Terrapene carolina*	*Duchesnea indica*
[18]	Braun and Brooks 1987	*Terrapene carolina*	*Fragaria virginiana*
[18]	Braun and Brooks 1987	*Terrapene carolina*	*Prunus serofina*
[18]	Braun and Brooks 1987	*Terrapene carolina*	*Vitis aestivalis*
[18]	Braun and Brooks 1987	*Terrapene carolina*	*Vitis vulpina*
[18]	Braun and Brooks 1987	*Terrapene carolina*	*Sambucus canadensis*
[21]	Cobo and Andandreu 1988	*testudo graeca*	*Hypochaeris glabra*

[21]	Cobo and Andandreu 1988	*Testudo graeca*	*Spergula arvensis*
[21]	Cobo and Andandreu 1988	*Testudo graeca*	*Ornithophus sativus*
[21]	Cobo and Andandreu 1988	*Testudo graeca*	*Briza maxima*
[21]	Cobo and Andandreu 1988	*Testudo graeca*	*Rumex bucephalophorus*
[22]	Kimmons and Moll 2010	*Trachemys scripta*	*Morus sp.*
[22]	Kimmons and Moll 2010	*Trachemys scripta*	*Echinochloa crus-galli*
[22]	Kimmons and Moll 2010	*Trachemys scripta*	*Rumex crispus*
[23]	Kennet and Russel-Smith 1993	*Elseya dentata*	*Terminalia erythrocarpa*
[23]	Kennet and Russel-Smith 1993	*Elseya dentata*	*Terminalia microcarpa*
[23]	Kennet and Russel-Smith 1993	*Elseya dentata*	*Ficus racemosa*
[23]	Kennet and Russel-Smith 1993	*Elseya dentata*	*Syzygium forte*
[23]	Kennet and Russel-Smith 1993	*Elseya dentata*	*Pandanus aquaticus*
[23]	Kennet and Russel-Smith 1993	*Elseya dentata*	*Cyclophyllum schultzii*
[23]	Kennet and Russel-Smith 1993	*Elseya dentata*	*Nauclea orientalis*

Appendix 7: Time discretisation for the activity periods of Aldabra giant tortoises (*Aldabrachelys gigantea*) on Aldabra Atoll to account for the non-linear relationship between time and activity. We discretised continuous time into four periods (I– IV), following the overall activity turning points through time, and comprising 06:00–08:00, 08:15–13:30, 13:30–17:30 and 17:45–20:00, respectively



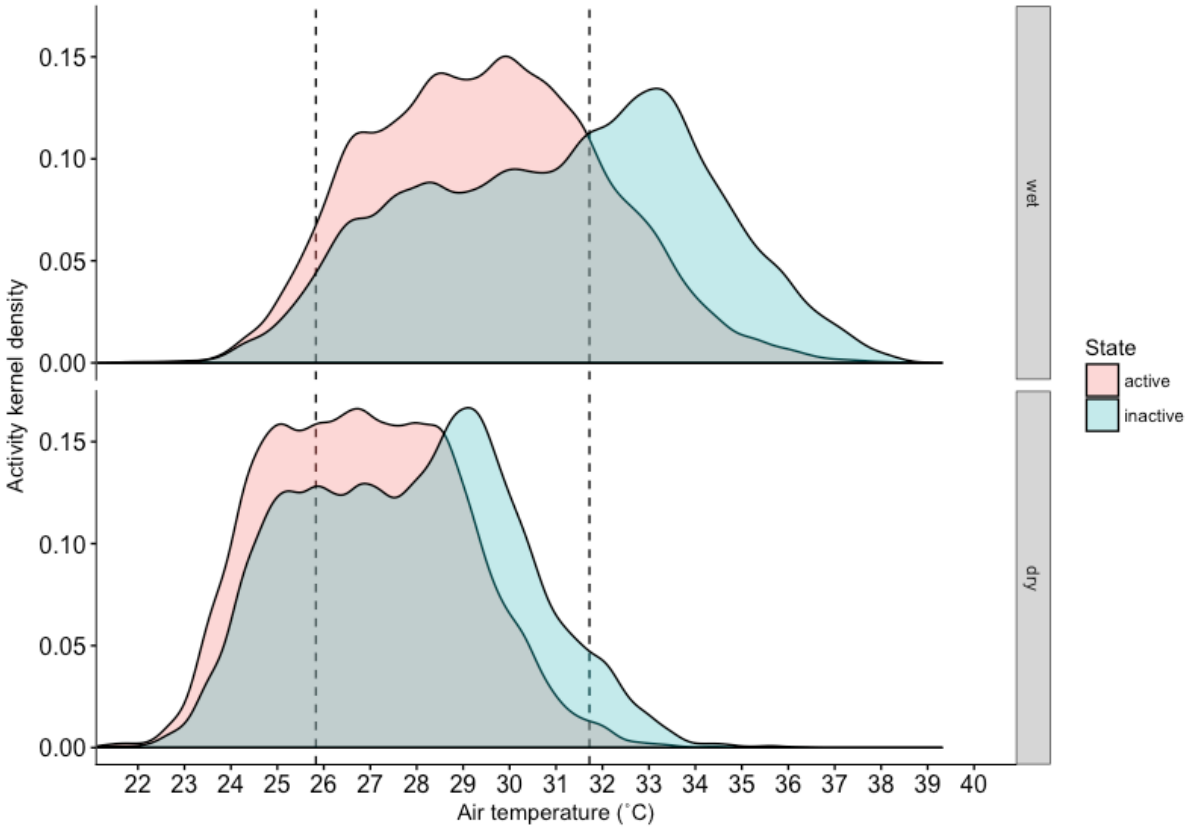
Appendix 8: Time discretisation for the thermoregulation periods of Aldabra giant tortoises (*Aldabrachelys gigantea*) in each trial to account for the non-linear relationship between time and core body temperature (T_{bc}). Continuous time was discretised into three periods (I, II, and III) comprising the morning period when tortoises are cooling down, the morning-afternoon period when tortoises are heating up, and the night period when tortoises start to cool down, respectively, for each trial independently. Lines depict the Tbc of each individual of a given mass (legend) per trial, with the 95% CI by local regression, loess.



Appendix 9: Results of the mixed-effects model on the influence of air temperatures on the activity of Aldabra giant tortoises on Aldabra Atoll.

Fixed effect	Estimate	SE	*p*-value
Intercept	0.87	0.30	0.003
$year_{II}$	0.01	0.05	0.89
$time_{II}$	10.03	0.24	< 0.001
$time_{III}$	3.74	0.26	< 0.001
$time_{IV}$	-10.22	0.28	< 0.001
T_{air}	-0.04	0.01	< 0.001
$season_{dry}$	3.09	0.16	< 0.001
$time_{II}$: T_{air}	-0.34	0.01	< 0.001
$time_{III}$: T_{air}	-0.15	0.01	< 0.001
$time_{IV}$: T_{air}	0.33	0.01	< 0.001
$season_{dry}$: T_{air}	-0.13	0.01	< 0.001

Appendix 10: Activity seasonality of giant tortoises (*Aldabrachelys gigantea*) on Aldabra Atoll in relation to air temperature. Vertical lines depict the air temperature range at which activity is maximised when the two seasons are combined.



Appendix 11: Summary statistics of the external body temperatures (T_{be}) of Aldabra giant tortoises (*Aldabrachelys gigantea*), with different size and body mass, exposed to different thermal environments.

Skin folds

Tortoise (mass)	Study	Mean	Min	Max	Range	±SD
JVS (14kg)	ZRH Winter	18.5	16.1	21.4	5.3	1.5
JVL (19kg)	ZRH Winter	19.8	17.1	21.5	4.4	1.0
HMA (100kg)	ZRH Winter	20.7	18.7	22.0	3.3	0.8
SBY (140kg)	ZRH Winter	19.7	18.6	21.1	2.5	0.6
BBY (180kg)	ZRH Winter	19.8	18.3	21.3	3.0	0.7
HMA (100kg)	ZRH Summer	29.6	25.2	33.4	8.2	2.5
SBY (140kg)	ZRH Summer	29.2	25.5	33.4	7.9	2.3
BBY (180kg)	ZRH Summer	28.5	24.2	33.0	8.8	2.0
BEL (39kg)	Aldabra	28.6	25.0	33.0	8.0	2.1
WIL (35kg)	Aldabra	29.7	23.7	34.0	10.3	2.6
UNM (48kg)	Aldabra	28.7	24.2	33.5	9.3	2.2
CFK (61kg)	Aldabra	28.8	24.9	33.5	8.6	2.2
LDX (97kg)	Aldabra	29.6	25.6	33.7	8.1	2.0

Extremities

Tortoise (mass)	Study	Mean	Min	Max	Range	±SD
JVS (14kg)	ZRH Winter	18.3	15.4	22.0	6.6	1.8
JVL (19kg)	ZRH Winter	19.4	16.8	21.9	5.1	1.3
HMA (100kg)	ZRH Winter	20.0	17.2	21.9	4.7	1.3
SBY (140kg)	ZRH Winter	19.2	17.3	21.0	3.7	0.9
BBY (180kg)	ZRH Winter	19.4	16.6	21.4	4.8	1.1
HMA (100kg)	ZRH Summer	29.3	21.9	37.4	15.5	3.7
SBY (140kg)	ZRH Summer	29.1	23.0	37.8	14.8	3.6
BBY (180kg)	ZRH Summer	28.5	22.8	37.7	14.9	3.3
BEL (39kg)	Aldabra	28.7	24.7	33.3	8.6	2.1
WIL (35kg)	Aldabra	29.4	21.4	34.4	13.0	2.9
UNM (48kg)	Aldabra	28.5	22.5	33.5	11.0	2.4
CFK (61kg)	Aldabra	28.7	24.4	33.5	9.1	2.3
LDX (97kg)	Aldabra	29.5	25.6	33.5	7.9	2.1

Carapace

Tortoise (mass)	Study	Mean	Min	Max	Range	±SD
JVS (14kg)	ZRH Winter	18.6	14.7	23.2	8.5	2.2
JVL (19kg)	ZRH Winter	19.5	16.0	22.3	6.3	1.9
HMA (100kg)	ZRH Winter	19.5	15.8	22.4	6.6	1.9
SBY (140kg)	ZRH Winter	19.1	15.6	23.2	7.6	1.8
BBY (180kg)	ZRH Winter	19.2	15.4	22.7	7.3	2.0

HMA (100kg)	ZRH Summer	30.8	19.8	44.2	24.4	6.5
SBY (140kg)	ZRH Summer	30.2	19.8	42.7	22.9	6.4
BBY (180kg)	ZRH Summer	29.9	20.6	41.9	21.3	6.1
BEL (39kg)	Aldabra	28.9	22.9	38.5	15.6	3.2
WIL (35kg)	Aldabra	28.9	20.6	41.6	21.0	4.5
UNM (48kg)	Aldabra	28.1	20.6	37.3	16.7	3.7
CFK (61kg)	Aldabra	28.9	22.9	38.3	15.4	3.4
LDX (97kg)	Aldabra	29.9	24.1	47.1	23.0	4.1

Appendix 12: Results of the mixed effects model of Aldabra giant tortoise core body temperature.

Fixed effects	Estimate	SE	*p*-value
Intercept	14.79	0.50	<0.001
$Trial_{ZRH\ summer}$	7.91	0.57	<0.001
$Trial_{Aldabra}$	5.73	0.51	<0.001
$time_{II}$	-0.26	0.03	<0.001
$time_{III}$	1.32	0.02	<0.001
T_{air}	0.36	0.01	<0.001
mass	0.03	0.00	<0.001
T_{air}:*mass*	0.00	0.00	<0.001

Appendix 13: Details for the data used for the literature review on Testudinidae core body temperature in relation to air temperature and mass (**Excel file**).

Available at:
http://onlinelibrary.wiley.com/store/10.1002/ece3.3766/asset/supinfo/ece33766-sup-0002-SupInfo.csv?v=1&s=4ed74cc597b477b93bd5dafc27a7651bedca5f28